TEMPORAL PATTERNS IN DISTRIBUTION AND HABITAT ASSOCIATIONS OF PREY FISHES AND SQUIDS

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ABSTRACT

The distribution and abundance of prey species provide an important link between physical oceanography and higher trophic level predators. Three types of organisms were used as indicators in these analyses, lanternfishes (family Myctophidae), flyingfishes (family Exocoetidae), and squids of the family Ommastrephidae. The latter two were further classified into three categories each, based on ecological and size characteristics. Data were collected during five years of the Monitoring of Porpoise Stocks Cruises (MOPS: 1986 - 1990) and three years of the *Stenella* Abundance Research Project (STAR: 1998 - 2000) during a total of 2,041 nightly stations when individuals were collected with dipnets and relative abundance estimated.

Distribution patterns illustrate three general features. First, at a large scale with respect to both space and time, taxa showed clear affinities for specific water masses. Second, there were clear interannual differences both with respect to overall distribution and location of areas of highest abundance, for each taxon. On a relatively fine scale (100s of km) it was not possible to predict the areas of highest density from year to year for any of the groups. Third, some groups exhibited greater interannual variation than others.

Relative abundance was analyzed using data from one ship only, in order to avoid the influence of potential sampling bias. Annual mean estimates show an apparent multi-year increase in numbers of several taxa from 1986 through 1990; estimates are again low in 1998 and increase through 2000. This pattern is evident for all fish taxa and, to a lesser extent, for squids. Because El Niño events occurred in both 1986/’87 and 1997/’98, we interpret this as evidence that populations of these taxa may be negatively affected by such events, gradually increasing subsequent to them.

Habitat association patterns were explored using Canonical Correspondence Analysis. A series of analyses were performed using all taxa and various subsets of habitat variables, the latter included oceanographic, geographic, and temporal variables. Three general results are relevant here. First, for any given year, oceanographic and geographic variables explained between 22 and 35% of the variance in relative abundance when all taxa were considered together. When considered individually, the analysis explained a high proportion of variance (25% or more) for three taxa, Myctophids (up to 76%), *Oxyporhamphus*, and large squid, and less for the remaining taxa. Second, for those three taxa for which the analysis explained a high proportion of variance, there were clear taxon-specific patterns in association with water mass types, and these association patterns remained broadly consistent across time. Within water masses, the strength of the association for any given taxon varied with time; this variation was higher within than between decades. Third, relative to all three types of habitat variables, oceanography and geography explained the vast majority of variance in relative abundance. When temporal variables were incorporated into the analysis, year explained a higher proportion of variance than decade, but added less than 3% to the total variance explained as compared to a few tenths of a percent for decade.

Our general conclusions for prey fishes and squids are the following. Strong year-to-year variation is evident in distribution and relative abundance; variation is less pronounced for habitat

association patterns. The magnitude of variation in all three measures of change (distribution, relative abundance, habitat association patterns) is as great or greater within a particular decade as between decades. And data support the idea of an El Niño effect at the population level with relative abundance at lowest values immediately following El Niño events, and gradually increasing over time subsequent to them.

INTRODUCTION

The distribution and abundance of prey species provide an important link between physical oceanographic parameters and higher marine vertebrates (marine birds and mammals) of the ETP. However, unlike planktonic organisms that are easily sampled with nets and Niskin bottles, or birds and mammals that can be visually surveyed, the abundance of bird and mammal prey is much more difficult to assess. This is because although most species are large enough to avoid nets, they are rarely seen at the surface, and an entire class of them are vertical migrators, present at the surface only at night. In an attempt to provide some measure of the variability of prey type and availability, and to better understand the relationship of these prey to other physical and biological parameters, we conducted nightly dipnet stations throughout the ETP to sample these potential prey items.

Flyingfish (Exocoetidae), lanternfish (Myctophidae), and ommastrephid squids (Ommastrephidae) are by far the most common prey organisms to be seen around a drifting vessel at night in the ETP; they are also easily caught with dipnets and relatively easy to census. They are important components in the diets of spotted and spinner dolphins (Robertson and Chivers 1997, Perrin 1998), and they comprise the majority of prey for many tropical seabirds (Ashmole and Ashmole 1967, Harrison *et al.* 1983). Because of these considerations, we investigated interannual and interdecadal patterns and variability in these prey types in order to see if they provided any clues to the variation we detected in marine bird and mammal occurrences. These investigations and analyses are to be interpreted within the context of the International Dolphin Conservation Program Act (ICPA). Relevant background information can be found in Ballance *et al.* (2002).

An independent scientific peer review of this work was administered by the Center for Independent Experts located at the University of Miami. Responses to reviewer's comments can be found in Appendix 2.

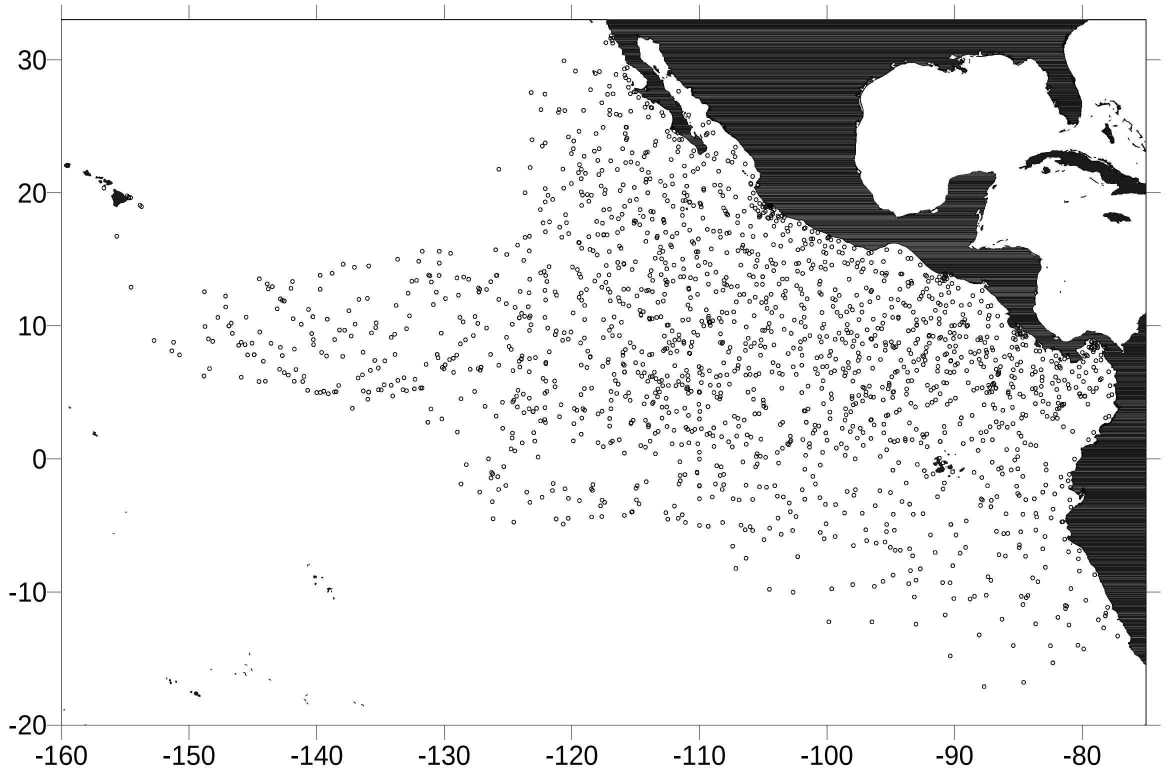
DATA COLLECTION METHODS

Weather and time permitting, surface organisms were collected every evening, and on some mornings, during one-hour dipnet stations. Sampling was conducted on one ship in 1986, and on two ships every year afterward, except in 1999 when three ships were used; the number of stations occupied per ship, per year throughout the study is given in Table 1. Figure 1 shows the spatial distribution of these staions for all ships and all years. Sampling stations usually coincided with CTD casts which occurred approximately 1 h after sunset and 1 h before sunrise. One or two 500-watt lamps were suspended over the side of the vessel to illuminate (and perhaps attract, in some cases) organisms in the water. One or, usually, two persons used long-handled dipnets to collect swimming organisms. In addition to organisms captured, we also recorded sighting information on the relative abundance of squids and fishes. The following codes were used to categorize the relative abundance of individuals observed for a given taxon: Code **1** - 1-3 individuals sighted; **2** - 4-8; **3** - 9-15; **4** - 16-50; **5** - 51-150; **6** - 150+; **7** - 1000s; **8** - present in unknown numbers; **9** - possibly present.

Table 1. Number of dipnet stations occupied per year on the research vessels during MOPS and STAR.

	1986	**1987**	**1988**	**1989**	**1990**	**1998**	**1999**	**2000**	**Total**
D.S. Jordan	95	98	131	124	110	99	122	159	1013
McArthur		131	101	102	144	133	138	128	940
Endeavor						88			88
Total	95	229	232	226	254	320	260	287	2041

Figure 1. Spatial distribution of dipnet stations from all ships, all years.



Squids were comprised almost entirely of two ommastrephid species: *Docidicus gigas* and *Sthenoteuthis oualaniensis* - since these species could not always be reliably identified *in situ*, we combined them for analysis. Other species of squids (*e.g.*, *Onychoteuthis banksi*, *Thysanoteuthis rhombus*) were so rarely seen and so readily identifiable in the field, that we have ignored them in this analysis. Squids were recorded as one of three size categories: Large (mantle length greater than 8 inches), Medium (mantle length 3-8 inches) and Small (mantle length less than 3 inches).

Flyingfish and myctophids were by far the most abundant, and typically the only, fish species present. As such, they were the only fish taxa analyzed. All myctophids were combined under a single taxon code. Flyingfish (Exocoetidae) were coded in the following categories: short-winged flyingfish (*Oxyporhamphus micropterus*), two-winged flyingfish (*Exocoetus monocirrhus*, *E. volitans*, *E. obtusirostris*), and unidentified four-winged flyingfish (*Cypselurus* spp., *Cheilopogon* spp., *Hirundichthys* spp., *Prognichthys* spp., *Parexocoetus brachypterus*). Although this last category contains 5 genera and at least 16 species of flyingfish, they are morphologically and ecologically all very similar. For example, the adults of nearly all these species range between 150 and 200 mm in fork length, and they all live in the upper few m of the water column. All other fish caught were given their own separate codes depending on how common they were, with most coded as "unidentified fish"; these were collected for later identification.

For each sampling station, we also recorded moon phase, cloud cover, sea surface temperature and salinity, sea state (Beaufort), and start and stop times. Nearly all of the sampling stations coincided with the nightly (or in a few cases, morning) CTD casts which provided us with detailed data on temperature and salinity profiles, as well as productivity measurements for each station.

ANALYSES AND RESULTS

For all results that follow, we used data from stations when sea state was Beaufort 4 or lower; data collected in higher sea states were excluded because these conditions compromised our ability to detect and capture surface fauna. We also converted the categorical abundance codes listed above to single values as follows: Code 1 (1-3 sighted) = 2 individuals; Code 2 (4-8 sighted) = 6 individuals; Code 3 (9-15 sighted) = 12 individuals; Code 4 (16-50 sighted) = 32 individuals; Code 5 (51-150 sighted) = 100 individuals; Code 6 (150+ sighted) = 500 individuals; Code 7 (1000s sighted) = 1000 individuals. These values were used in the following analyses of distribution, relative abundance, and habitat associations.

I. DISTRIBUTION AND RELATIVE ABUNDANCE

Analyses

Using the software program *Surfer 7*, we made distribution plots that contoured the relative abundance values at each dipnet station. We used the default option of kriging for contouring these values.

We calculated a mean relative abundance value for each taxon for each survey year by simply calculating the mean of all values recorded at dipnet stations that year. The distribution of tracklines during MOPS and STAR was broadly similar for the *David Starr Jordan* (see Figure 2 in Ballance *et al.* 2002) in that this ship primarily surveyed the area east of 120°W and north of the equator each year. The same was not true for the *McArthur*; its trackline distribution varied significantly between MOPS and STAR years (Figure 2 in Ballance *et al.* 2002). Because of this, and to avoid the influence of this sampling bias on our relative abundance estimates, we used only data collected aboard the *David Starr Jordan* to calculate these yearly means.

Results and Discussion

Annual distribution patterns for each of the taxa are given in Figures 2 - 8. Figure 9 shows yearly means of relative abundance for each taxon. Several patterns are immediately apparent.

1. Each taxon shows clear interannual differences both with respect to overall distribution

and location of areas of highest abundance. On a relatively fine scale (100s of km) it was not possible to predict the areas of highest density from year to year for any of the groups.

2. Despite the interannual differences, on a larger temporal scale, taxa showed clear affinities for different water masses. For example, *Oxyporhamphus micropterus*, medium, and small squids (Figures 3, 7, and 8) consistently showed highest densities in waters adjacent to the coasts of Mexico and Central America (ETP core area), while *Exocoetus* spp. and unidentified 4-wing flyingfish (Figures 4 and 5) also had highest densities in the far eastern Pacific but were displaced somewhat offshore of the core area. Myctophids (Figure 2) avoided the core area altogether and had highest densities further offshore and to the south.

3. Although the overall patterns within each taxon are largely preserved from year to year, some groups showed more annual variation than others. Large squids (Figure 6) for example, show considerable variation in distribution and abundance from year to year, perhaps reflecting the fact that they may be several years old, while most of the fish taxa represented here are annuals.

4. Perhaps the most intriguing pattern in the figures is an apparent multi-year increase in numbers of several taxa from 1987 (the first year with two vessels collecting data) through 1990; then the numbers drop down again in 1998 and increase through 2000. This pattern is evident for all fish taxa (Figures 2 - 5 and Figure 9) and, to a lesser extent, for squids. In most cases, the most dramatic change in relative abundances occurs in the drop between 1990 and 1998, although by 2000, relative abundances have increased again. This three-year series (1998-2000) may be showing the effects and recovery of the 1998 La Niña event.

Figure 2. Distribution of myctophids. Color contours represent numbers of individuals sighted during dipnet stations. Locations of dipnet stations are represented by dark points.

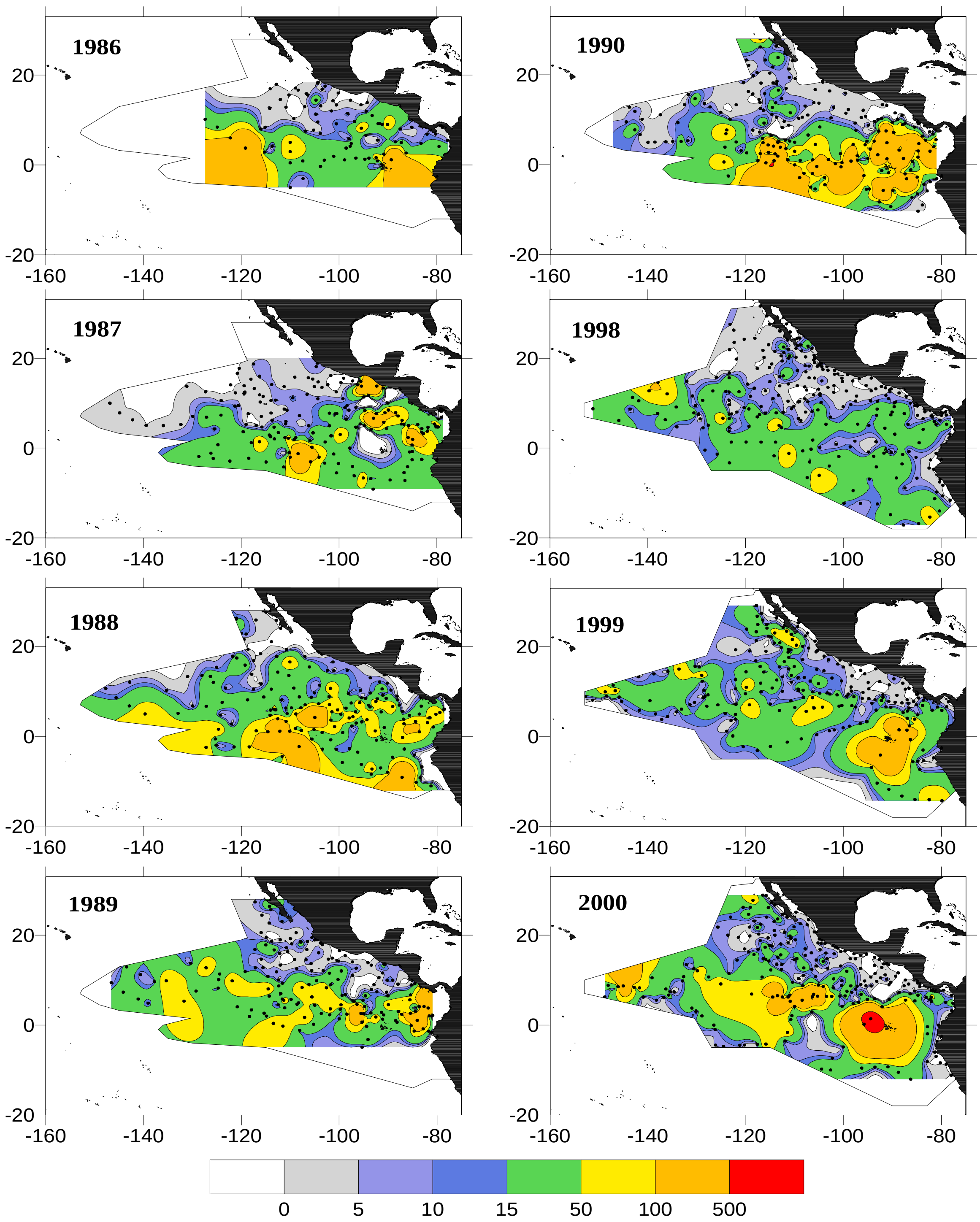


Figure 3. Distribution of *Oxyphorhamphus*. Color contours represent numbers of individuals sighted during dipnet stations. Locations of dipnet stations are represented by dark points.

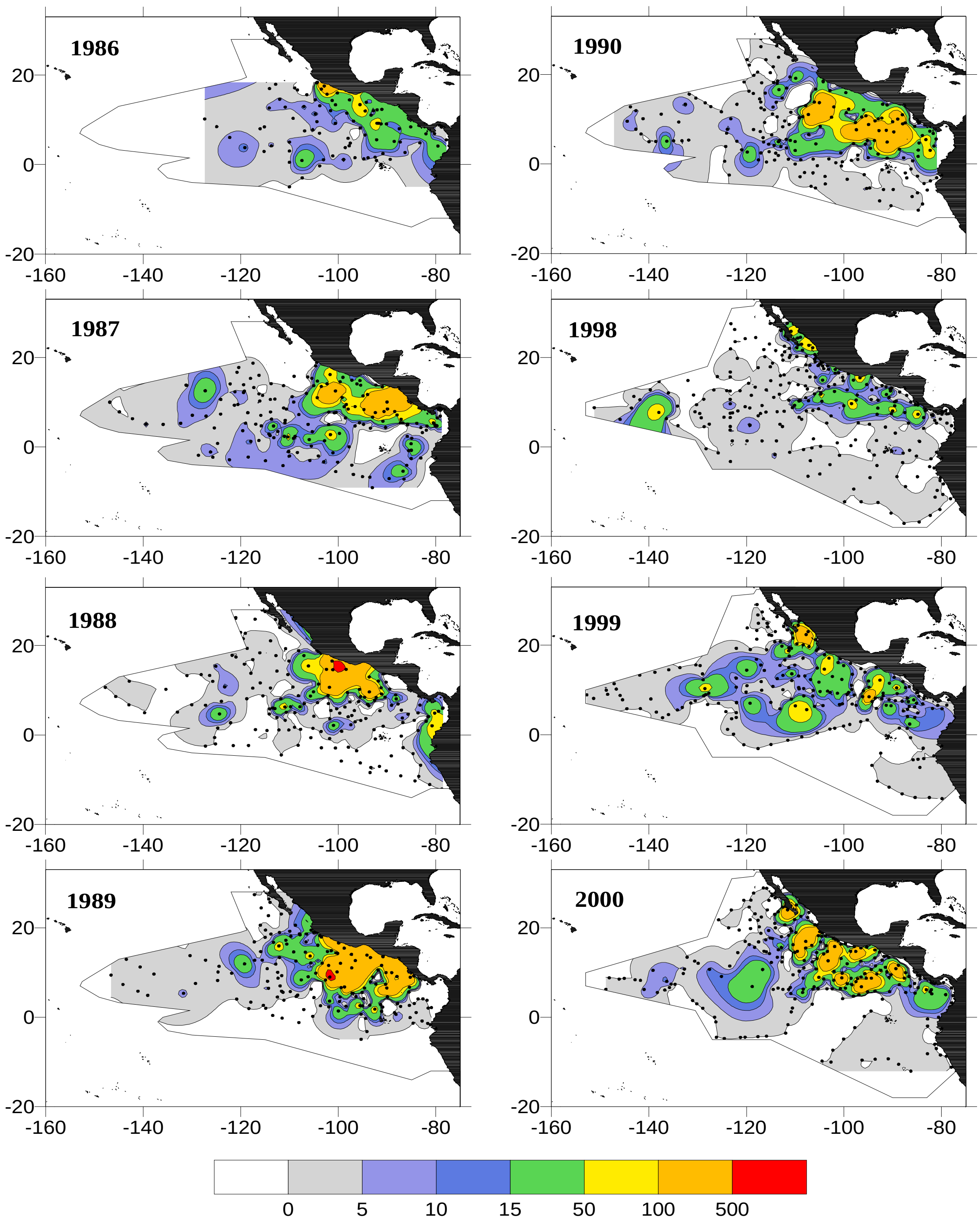


Figure 4. Distribution of *Exocoetus*. Color contours represent numbers of individuals sighted during dipnet stations. Locations of dipnet stations are represented by dark points.

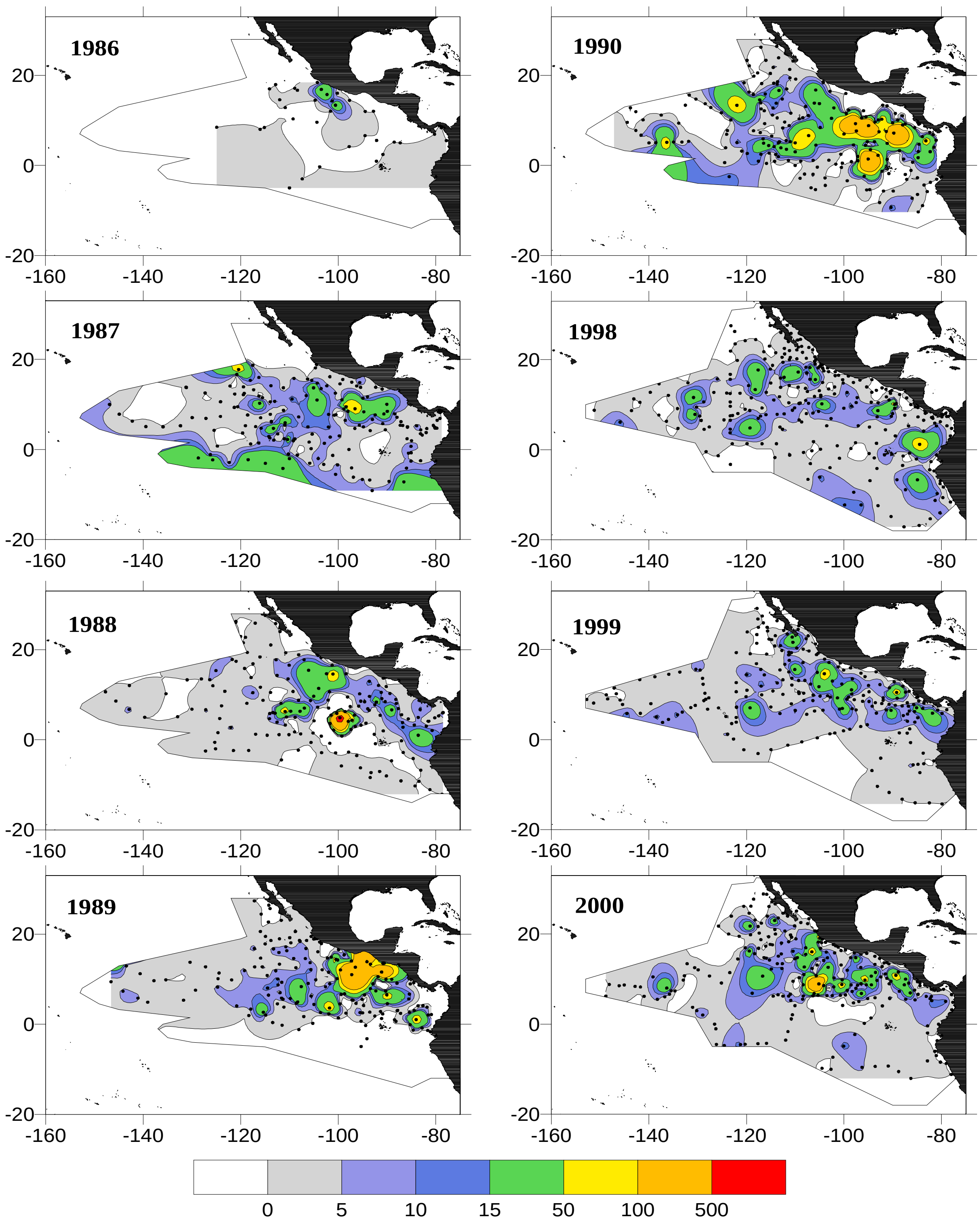


Figure 5. Distribution of four-winged flyingfish. Color contours represent numbers of individuals sighted during dipnet stations. Locations of dipnet stations are represented by dark points.

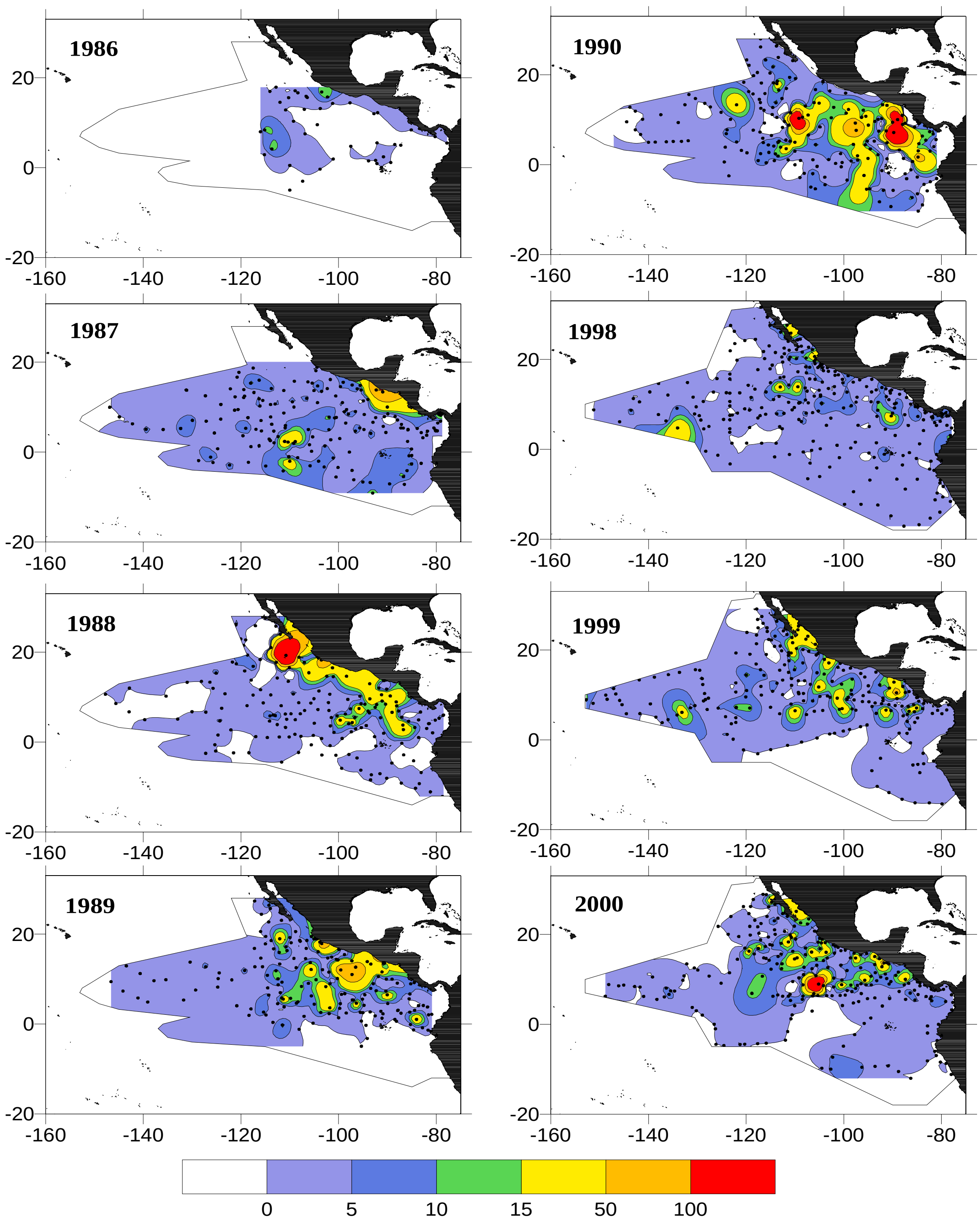


Figure 6. Distribution of large squids. Color contours represent numbers of individuals sighted during dipnet stations. Locations of dipnet stations are represented by dark points.

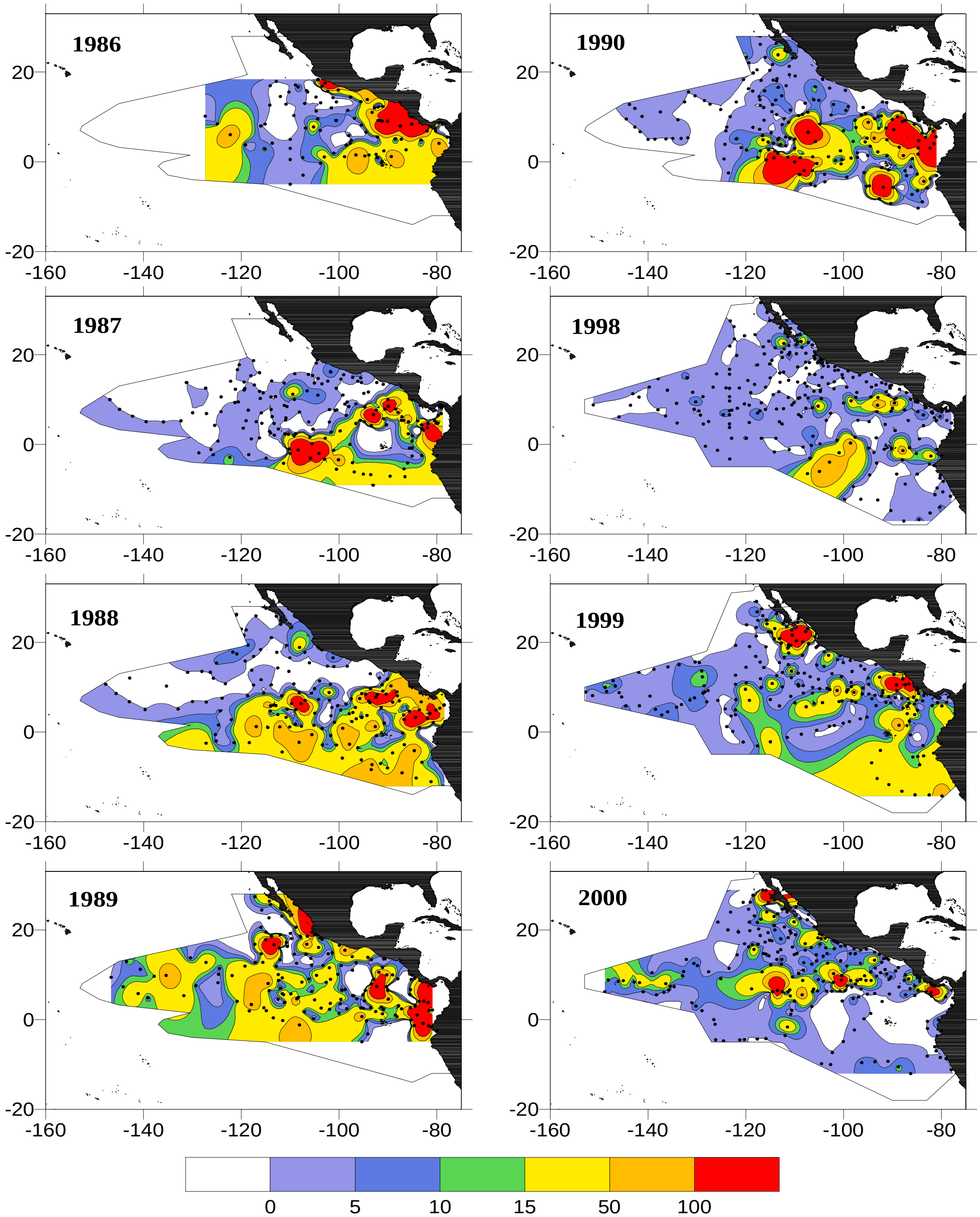


Figure 7. Distribution of medium squids. Color contours represent numbers of individuals sighted during dipnet stations. Locations of dipnet stations are represented by dark points.

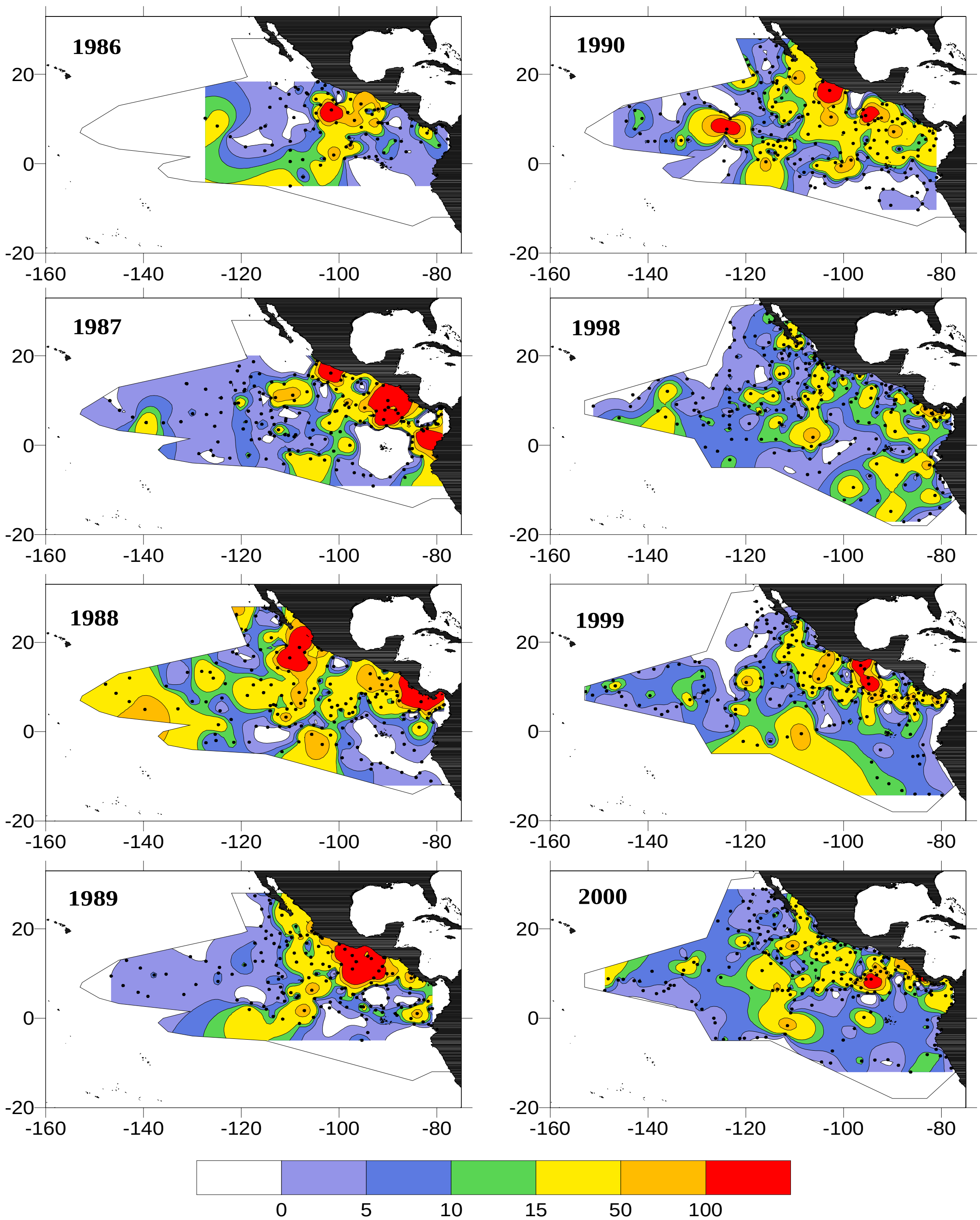


Figure 8. Distribution of small squids. Color contours represent numbers of individuals sighted during dipnet stations. Locations of dipnet stations are represented by dark points.

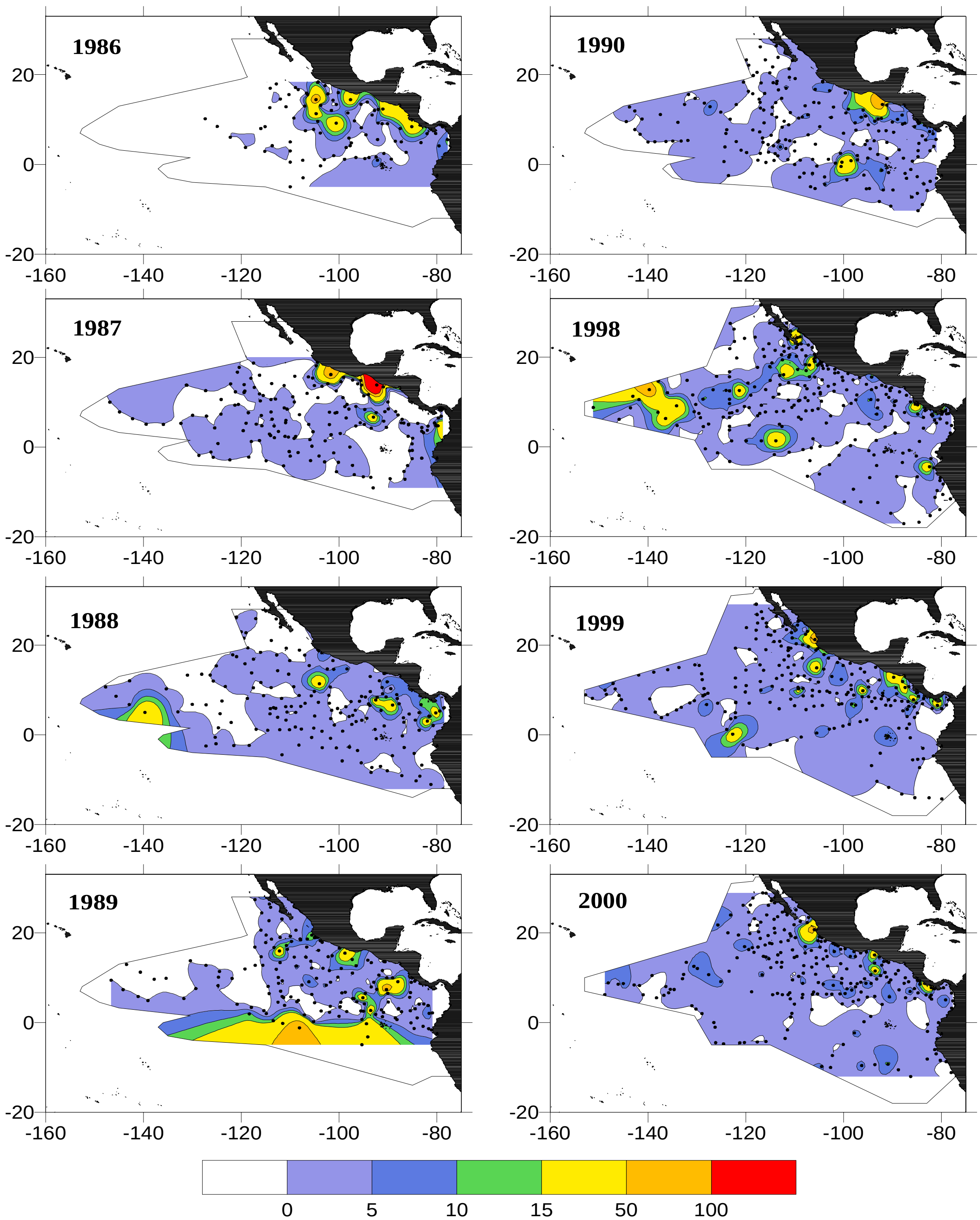
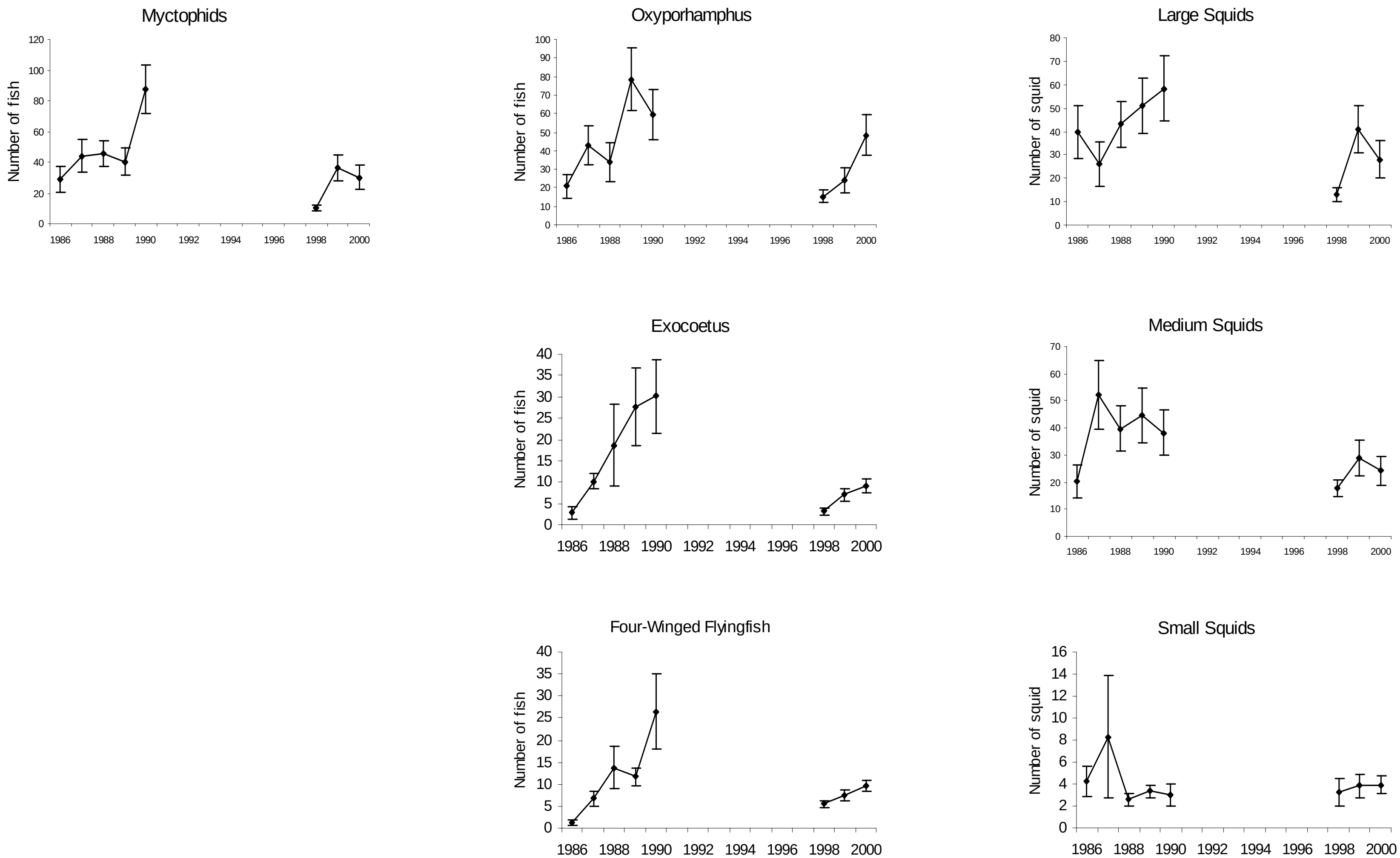


Figure 9. Yearly mean relative abundance (± SE) of prey fishes and squids sighted during nightly dipnet stations.



II. HABITAT RELATIONSHIPS

Analyses

Relationships between prey fishes and squid relative abundance and oceanic habitat were quantified using Canonical Correspondence Analysis (CCA, ter Braak 1986) and implemented by the program CANOCO 4 (ter Braak and Šmilauer 1998). CCA is a multivariate method of analysis which relates two independent sets of variables (here, relative abundance and environmental). Specifically, it relates community composition to variation in the environment by choosing ordination axes from taxon data which are linear combinations of environmental variables. The method assumes that response surfaces of taxa to environmental gradients are uni-modal, not linear, and that sampling includes the entire range of each variable so as to completely sample a taxon's range of response. CCA is relatively robust to these assumptions, and is particularly appropriate for data sets containing many zero values, a feature typical of abundance data sets, including the present data on prey fishes and squids.

Results of CCA can be used to identify habitat types from integrated combinations of individual habitat variables, to identify taxon-specific habitat preferences, and to identify relative similarity between taxa with respect to these preferences. Here we use CCA to investigate temporal patterns in these three measures by comparing time series of ordination results performed with data from single years, and by integrating data from all years into a single ordination (see below).

To quantify oceanic habitat, we chose a suite of seven oceanographic variables: sea surface temperature, sea surface salinity, surface chlorophyll concentration, sigma-t (an index of water density based on temperature and salinity), thermocline depth (the depth of maximum temperature gradient, calculated with an algorithm that ensured the temperature gradient extended through multiple data points), thermocline strength (the value of the maximum temperature gradient), and mean concentration of chlorophyll in the euphotic zone (the integrated chlorophyll concentration from the surface to the euphotic zone depth, estimated as in Morel 1988). We added two geographic variables to this set, latitude and longitude, for a total of nine habitat variables. Previous studies have shown that these variables are important in understanding distribution and abundance of seabirds and cetaceans (Reilly and Fiedler 1994, Ballance *et al.* 1997, Spear *et al.* 2001).

We used point values for each oceanographic variable as determined by a CTD cast (conducted simultaneously with each dipnet station). These values plus ship position (latitude and longitude) were used to represent habitat sampled during each station. Surface and mean euphotic zone chlorophyll concentration values were log-transformed and all oceanographic and geographic variables were standardized to zero mean and unit variance to remove effects from differing scales of measurement.

Each CCA was run using biplot scaling of interspecies differences (where taxon scores are the weighted averages of sample scores) so that each taxon's point in resulting ordination diagrams (see Figure 15) is at the center of its niche and represents most accurately the dissimilarities between the occurrence patterns of different taxa. Relative abundance data were not transformed prior to analysis, although rare taxa were down-weighted. The result of these treatments is that extreme density values for a given taxon will tend to have relatively high influence on the ordination results, but the influence of rare taxa on the ordination will not be large relative to abundant taxa.

In order to investigate effects of interannual variation, we added ten additional categorical variables, eight representing each survey year, and two representing each survey decade (MOPS and STAR). The significance of this variation was judged as in Reilly and Fiedler (1994) by first performing the CCA using oceanographic and geographic variables only, then again adding year/decade variables to investigate the additional contribution to variance explained (see below).

Results and Discussion

Years Analyzed Separately. The following results pertain to yearly ordinations performed with the seven oceanographic and two geographic variables included as measures of oceanic habitat.

The first four canonical axes explained between 22.5 and 35.3 percent of the variance in relative abundance, depending upon year (Table 2). This variance was largely accounted for by the first and second axes, with the first explaining approximately twice the amount of the second. Therefore, we confine subsequent investigations to these first two axes only. There is some interannual variation with respect to explained variance for each axis, and for the total.

Table 2. Ordination results from canonical correspondence analyses (CCA) of prey fishes and squid relative abundance and oceanic habitat as defined by seven oceanographic and two geographic variables. Each CCA was run with seven indicator taxa and data from one year only. Values represent percent of variance in relative abundance explained by each of the first four canonical axes. "Total" is cumulative percent variance in relative abundance explained by the first four axes.

	----------------- Canonical Axes -----------------				
	1	**2**	**3**	**4**	**Total**
1986	15.5	7.8	3.8	2.9	30.0
1987	13.3	10.3	5.5	2.4	31.5
1988	23.0	8.2	3.4	0.7	35.3
1989	18.4	5.6	2.3	0.9	27.2
1990	20.7	7.1	3.6	1.5	32.9
1998	16.9	7.5	2.7	1.3	28.4
1999	13.3	5.2	2.4	1.6	22.5

2000	19.4	9.1	2.8	0.6	31.9

The relationships between each taxon and habitat identified by the first two canonical axes were for the most part unimodal (Appendix 1). Thus a primary assumption of CCA was satisfied.

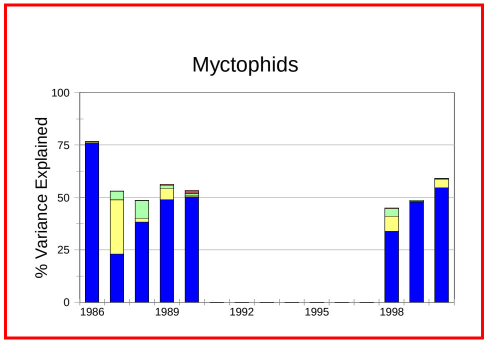
The explanatory power of the CCA varied with taxon. This is shown by Figure 10, which illustrates the following three patterns.

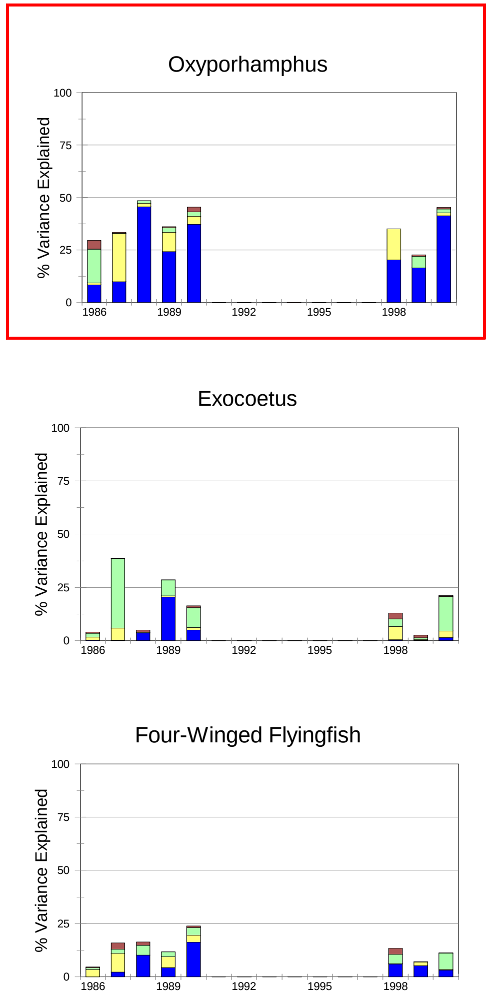
First, the ordinations explain a high proportion of variation in relative abundance for some taxa and little for others. In the former category are myctophids, where greater than 50% of variance was explained by the first four axes in seven of the eight years, and *Oxyporhamphus* and large squids, for which greater than 25% of variance was explained in most years. The ordinations explained much less of the variance in density for other taxa. Therefore, interpretations of ordination patterns will focus on those taxa in the former category, less on those in the latter.

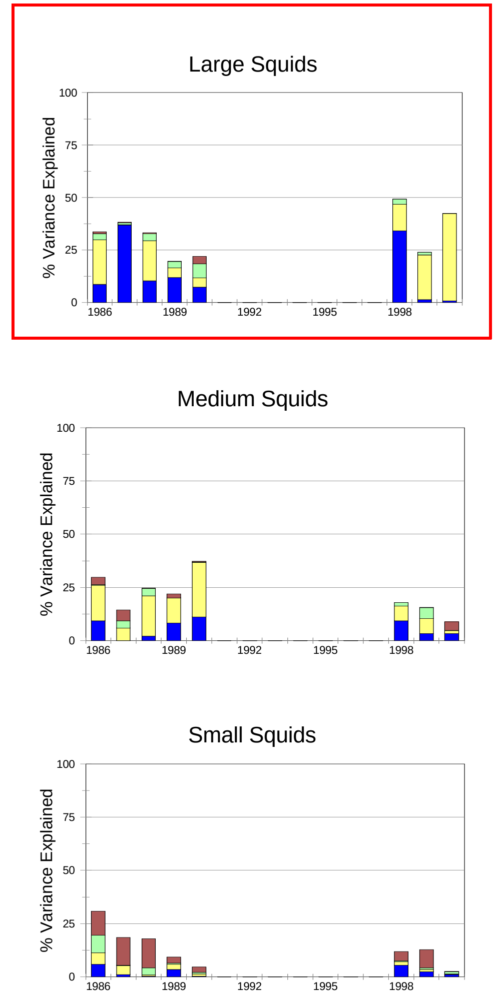
Second, there are distinct taxon-specific patterns with respect to which axes explain the greatest proportion of variance. Most notably, axis 1 explains a high proportion of variance for myctophids and *Oxyporhamphus*. But for large squids, axes 1 and 2 are each important, depending upon year. Investigations of taxon-specific patterns will therefore focus on the relevant axis, which will not necessarily be axis 1.

Third, whereas the above two patterns are broadly consistent over most years, there is some interannual variation with respect to the proportion of variance explained by the ordination, and the relative contributions of the first four axes to the total variance explained.

Figure 10. Temporal patterns in percent variance in relative abundance explained by each of the first four canonical axes: Blue = Axis 1; Yellow = Axis 2; Green = Axis 3; Brown = Axis 4, and all axes together (total bar height). The ordination explains 25% or more of the variance in density for most years for the 3 taxa outlined in red.







With respect to the scale of the entire study (all years), axis 1 defined the same general habitat type over time. This can be seen in Figure 11, where it is clear that the sign of scores for the 9 habitat variables on the first canonical axis is generally the same across all years. Scores are correlation coefficients when data are standardized, so that the magnitude of scores can be used as an indication of the importance of a particular environmental variable. Thus, axis 1 generally defines habitat with cool, saline, high density surface water, with deep and weak thermoclines, relatively low in chlorophyll content. On a shorter temporal scale, some interannual variation with respect to the contribution of each variable to this habitat type can be seen.

The same patterns apply to habitat defined by axis 2 (Figure 12). Over the entire study period, axis 2 generally defines the same habitat (high in chlorophyll with shallow thermoclines). Some interannual variation with respect to the contribution of each variable to this habitat is also apparent.

The first canonical axis was important in explaining variance for myctophids, and *Oxyporhamphus*, and, for some years, large squids (Figure 10). For these three taxa, the response to this habitat showed broadly similar patterns over time. Myctophids and large squids associated with it, and *Oxyporhamphus* avoided it (Figure 13). Again, there was some interannual variation in the degree of association.

The second canonical axis was important in explaining variance for large squids; less so for other taxa (Figure 10). Across all years, this taxon associated with habitat identified by axis 2 (Figure 14).

In summary: a) axes 1 and 2 were most informative, explaining between 20 and 30% of the variance in relative abundance; b) the habitat identified by axis 1 was generally the same across time, though there was some interannual variation with respect to the degree of contribution from specific oceanographic and geographic variables to this habitat type; c) patterns for axis 2 were similar (*i.e.* the habitat type was generally consistent across time with some interannual variation in degree of contribution from certain variables evident); d) for those taxa for which CCA explains a relatively high amount of variance, habitat association patterns were relatively consistent across time.

Figure 11. Scores of 7 oceanographic and 2 geographic habitat variables on canonical axis 1, by year. This axis explains between 13.3 (1987 and 1999) and 23.0% (1988) of the variance in relative abundance of the indicator taxa, depending upon year, and generally defines habitat with cool, saline, high density surface water, with deep and weak thermoclines, relatively low in chlorophyll content. Some interannual variation can be seen.

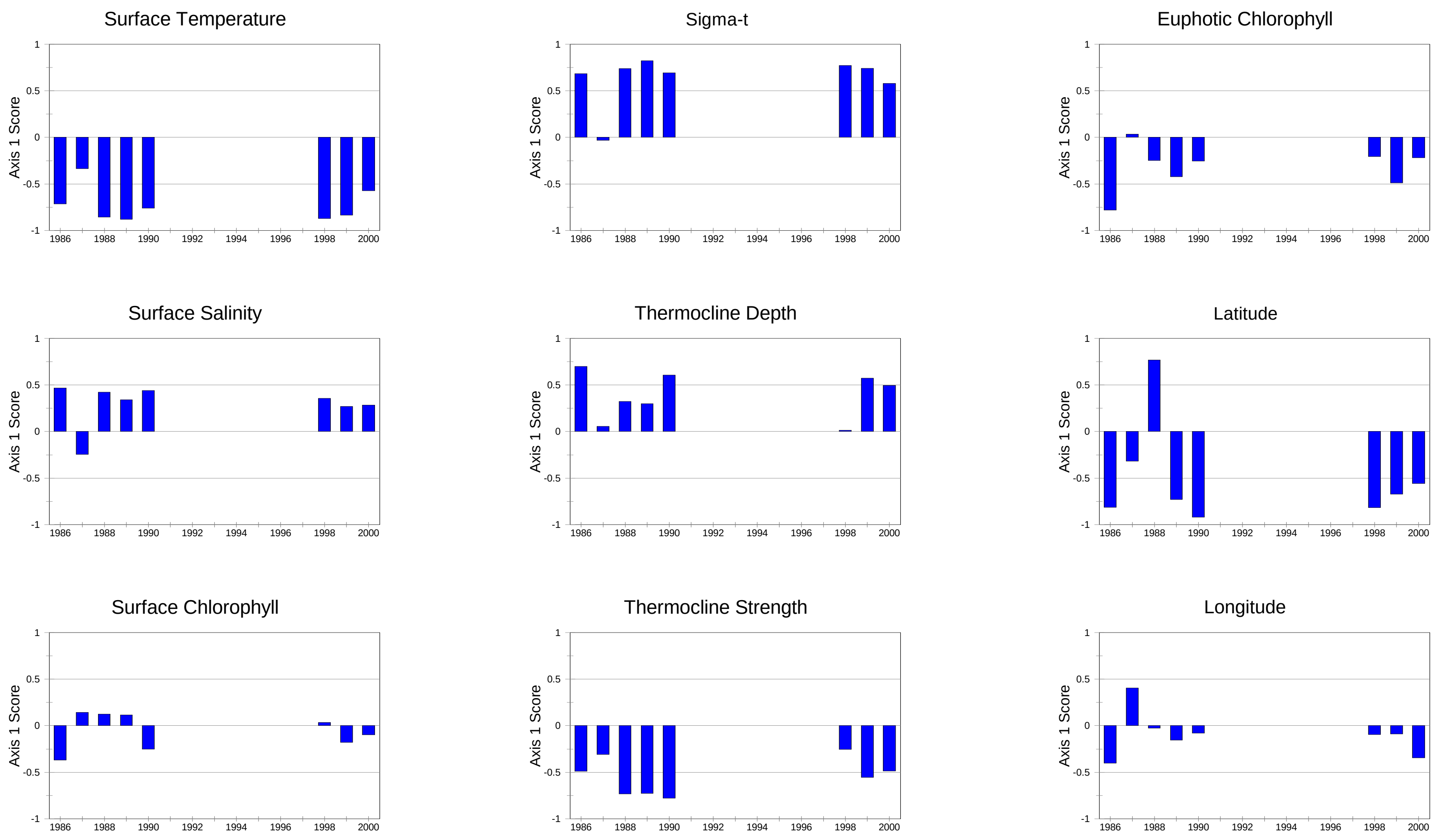


Figure 12. Scores of 7 oceanographic and 2 geographic habitat variables on canonical axis 2, by year. This axis explains between 5.2 (1999) and 10.3% (1987) of the variance in relative abundance of indicator taxa, depending upon year, and generally defines habitat high in chlorophyll with shallow thermoclines. Some interannual variation can be seen.

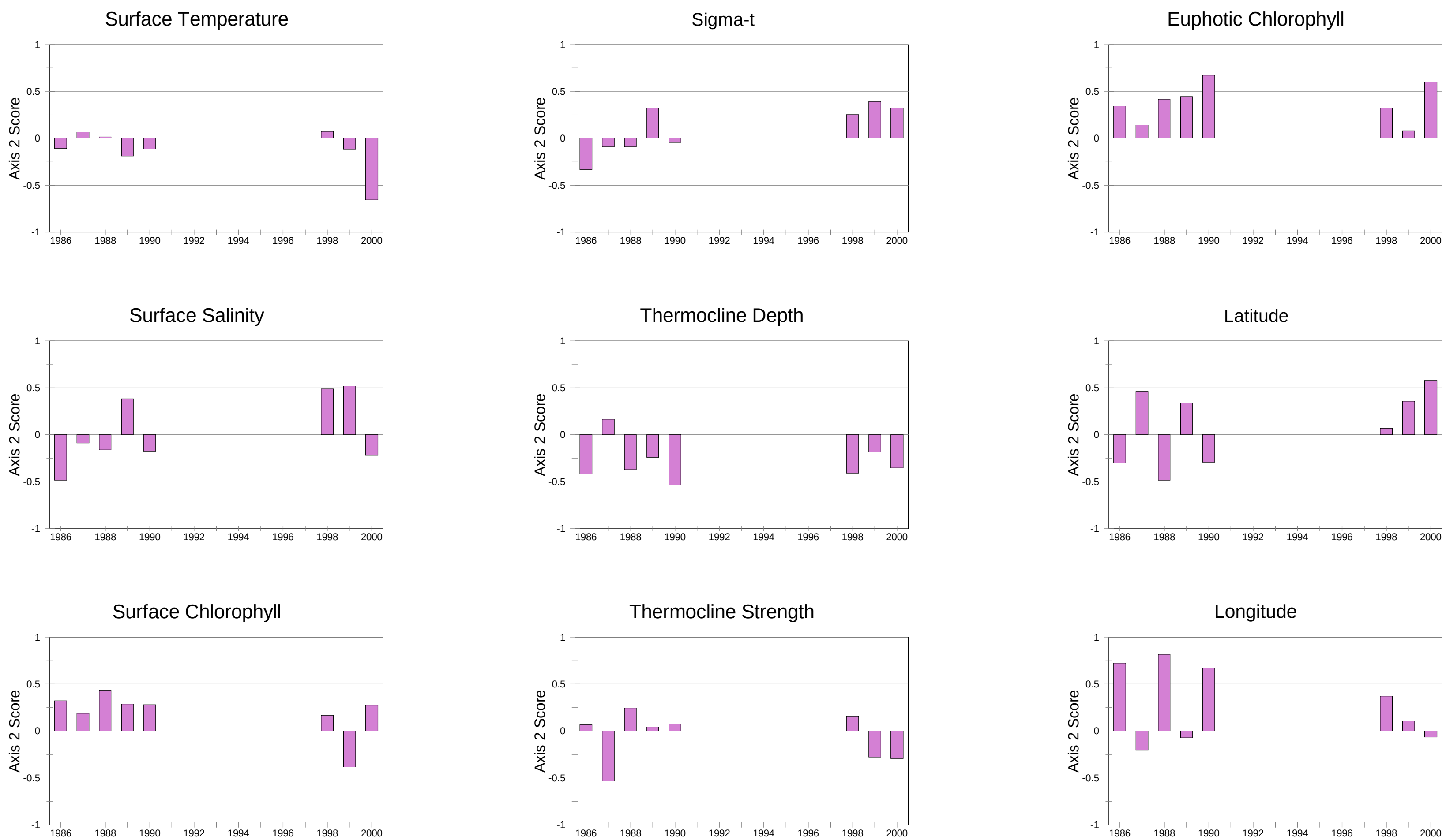
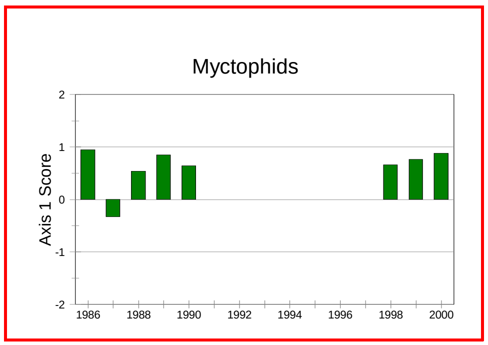
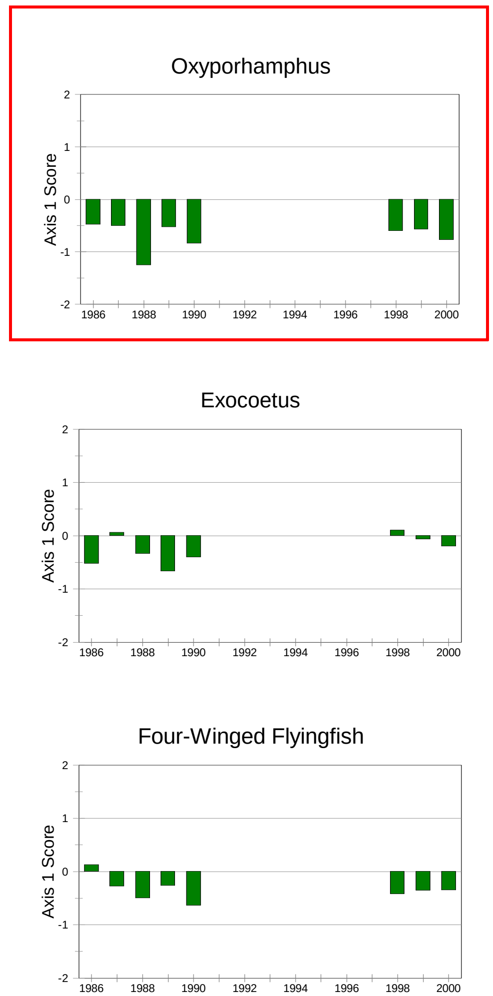


Figure 13. Scores of prey fishes and squids on canonical axis 1, by year. This axis is important in explaining variance for myctophids, *Oxyporhamphus*, and, for 1987 and 1990, large squids (see Figure 10). Association patterns with this habitat type are broadly consistent across time.





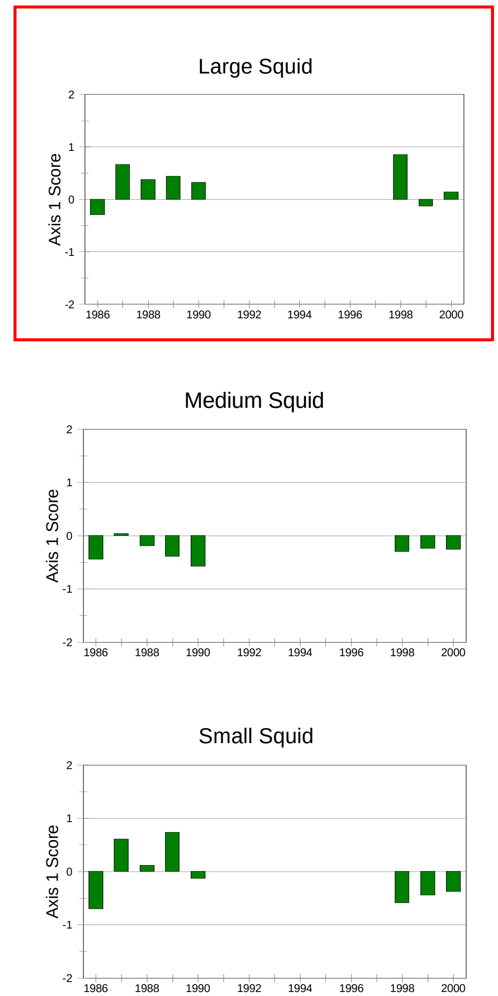
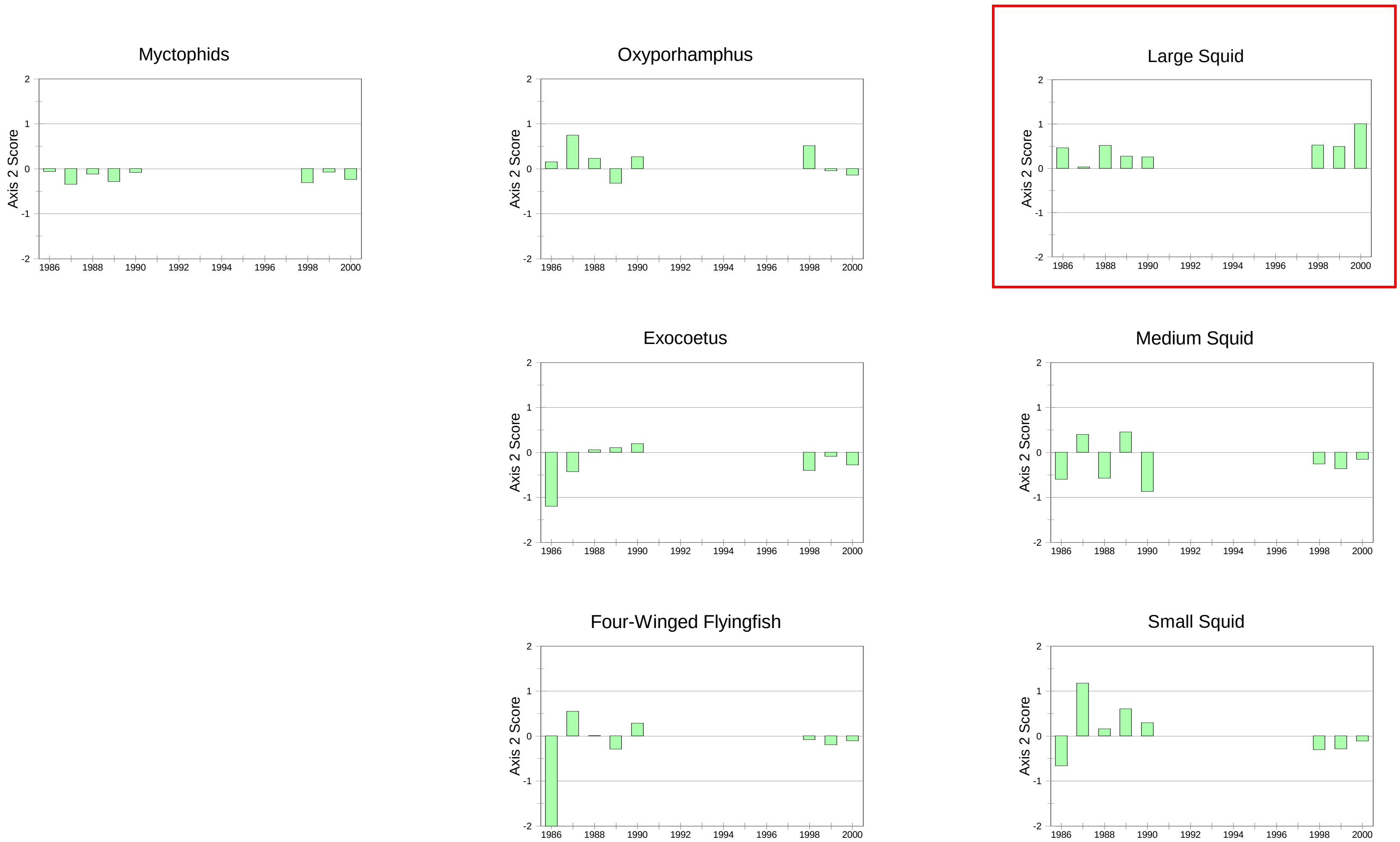


Figure 14. Scores of prey fishes and squids on canonical axis 2, by year. This axis is important in explaining variance for large squids (see Figure 12) and they consistently associated with this habitat type over time.



Years Analyzed Together. The following results pertain to ordinations performed with data from all years analyzed together using different sets of variables to represent habitat sampled. These sets are oceanographic, geographic, year, and decade variables.

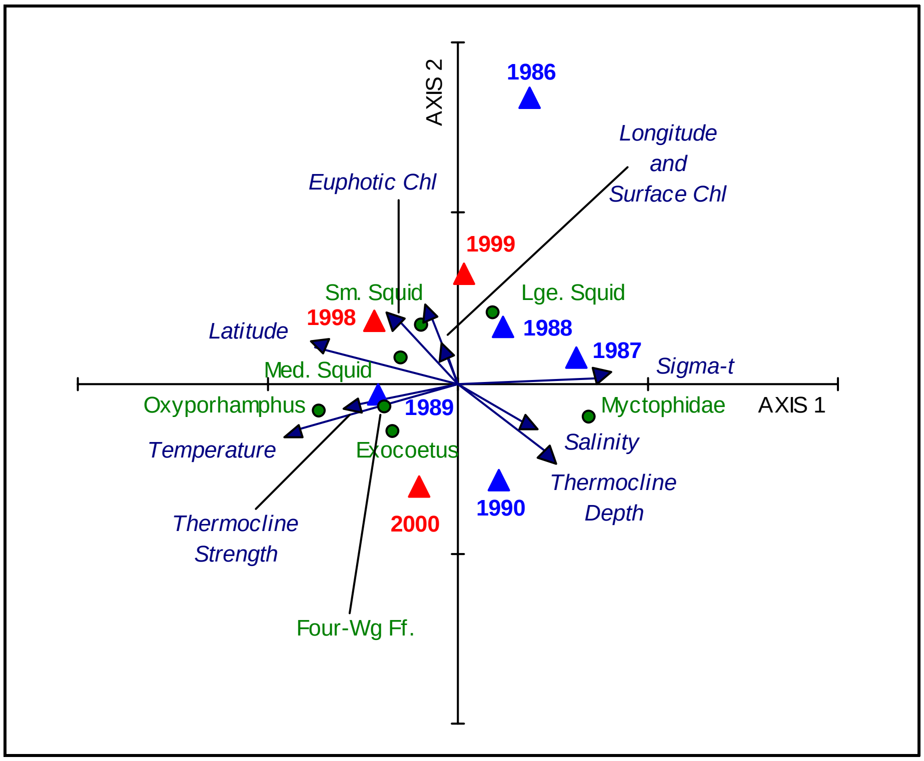
Relative to all four types of variables, oceanographic and geographic variables explained the highest proportion of variance in taxon data, a total of 16.9% (Table 3). Year explained a higher proportion of variance than decade, adding just over 1% to the total variance explained (year variables added to oceanographic and geographic) as compared to a few tenths of a percent (decade variables added to oceanographic and geographic). And the use of year variables as the only environmental variables explained just under 4% of the variance in relative abundance.

Table 3. Comparative ordinations from canonical correspondence analysis (CCA) of relative abundance of prey fishes and squids with respect to oceanic habitat as defined by oceanographic and geographic variables with different sets of interannual variables included. Each CCA was run with data from all years combined.

	---------------------------- Habitat Variables Included in Analysis ----------------------------				
	Oceanographic and Geographic	Oceanographic, Geographic, and Year	Oceanographic, Geographic, and Decade	All Variables	Year Only
% Variance in Relative Abundance Explained by First Four Axes	16.9	19.2	17.1	19.2	3.7

A final indication of the influence of temporal variation on the ordination can be seen with a biplot, typically used in CCA. Biplots illustrate the contribution of the environmental variables to the first two canonical axes, and taxon response to these same habitat axes. In the present case, the ordination of all years together results in a biplot representing an integrated mean of the influence of habitat variables on each canonical axis, and the relative location of each taxon with respect to these axes (Figure 15). The centroid points corresponding to each year have been added to the biplot. They clearly illustrate the interannual variation, but give no qualitative indication of any larger temporal scale trend.

Figure 15. Ordination biplot from CCA using oceanographic, geographic, and year variables to explain relative abundance of prey fishes and squids. Data from all years were combined. The contribution of oceanographic and geographic variables to each canonical axis can be interpreted from the direction and length of the lines corresponding to each variable. The response by each taxon is indicated by the points, which represent the center of that taxon's niche with respect to the habitat axes. Centroid values for each year are plotted and color-coded according to decade: red = MOPS, blue = STAR.



CONCLUSIONS

In general, these analyses and results indicate that variation within a particular decade (MOPS *versus* STAR) is greater than variation between adjacent years and between decades. These conclusions are supported by taxon-specific distribution patterns (Figures 2 - 8), which showed considerable variation from year to year, though areas of highest relative abundance were broadly consistent across time, and by relative abundance patterns for the fish taxa (Figure 9), which increased throughout each of the two survey periods (1986-1990 and 1998-2000) and decreased between the two. Taxa showed specific habitat association patterns that remained consistent over time (Figures 13 and 14), with some variation within decades evident. We believe this temporal scale variation may be explained by ENSO-scale perturbations which likely affect distribution and abundance of prey fishes and squids.

These conclusions mirror those of Fiedler and Philbrick (2002) in that regional effects of El Niño and La Niña are clearly visible in the oceanography of the ETP, and appear to dominate any longer-term (*i.e.* decadal-scale) signals.

ACKNOWLEDGMENTS

We sincerely thank the many biologists who collected data in the field, and the officers and crew of the research vessels *David Starr Jordan*, *McArthur,* and *Endeavor*. Jenna Borberg, Josh Fluty, Robert Holland, Kathy Hough, and Paula Olson provided invaluable assistance with data edit, processing, and figure preparation.

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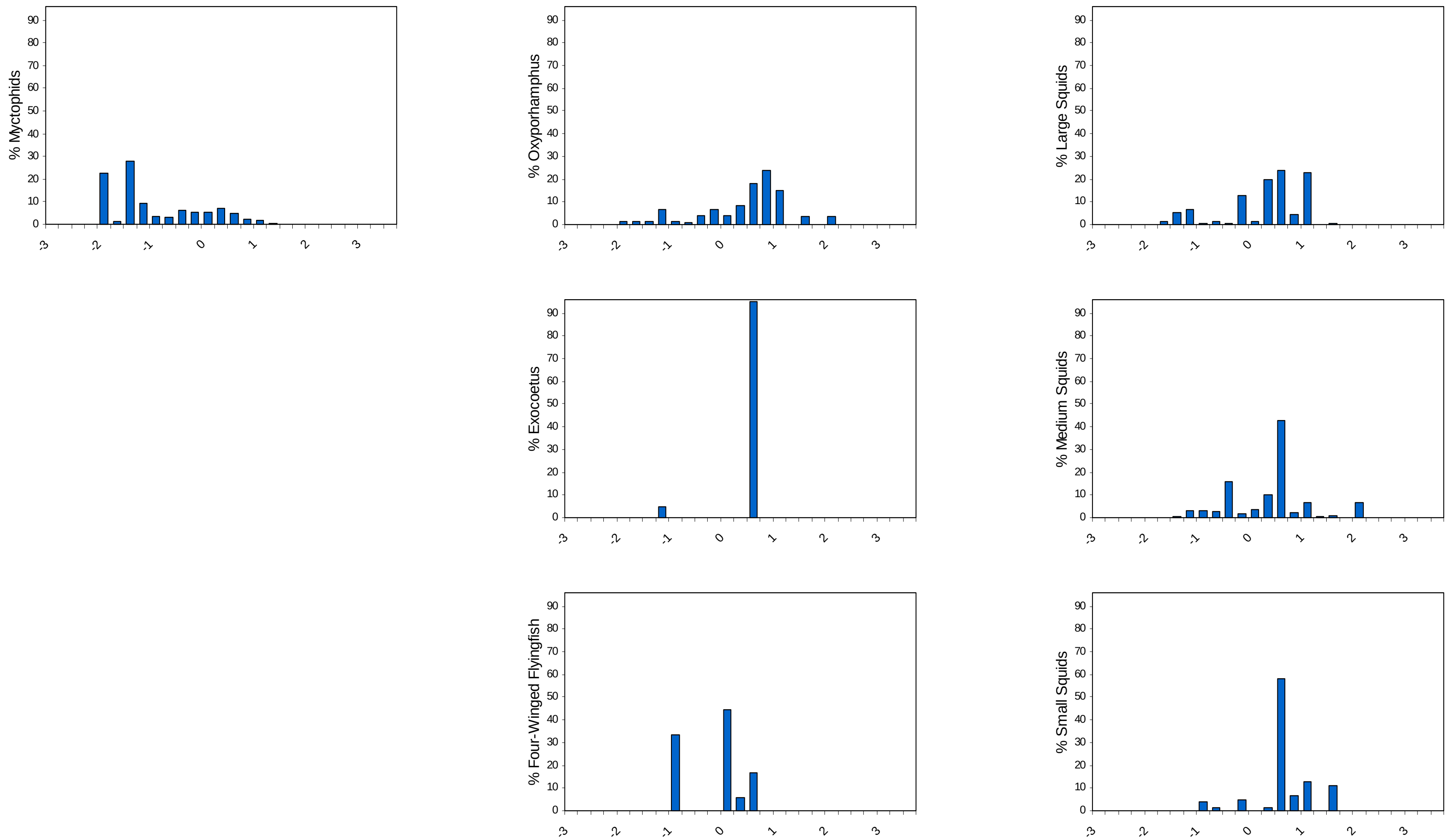
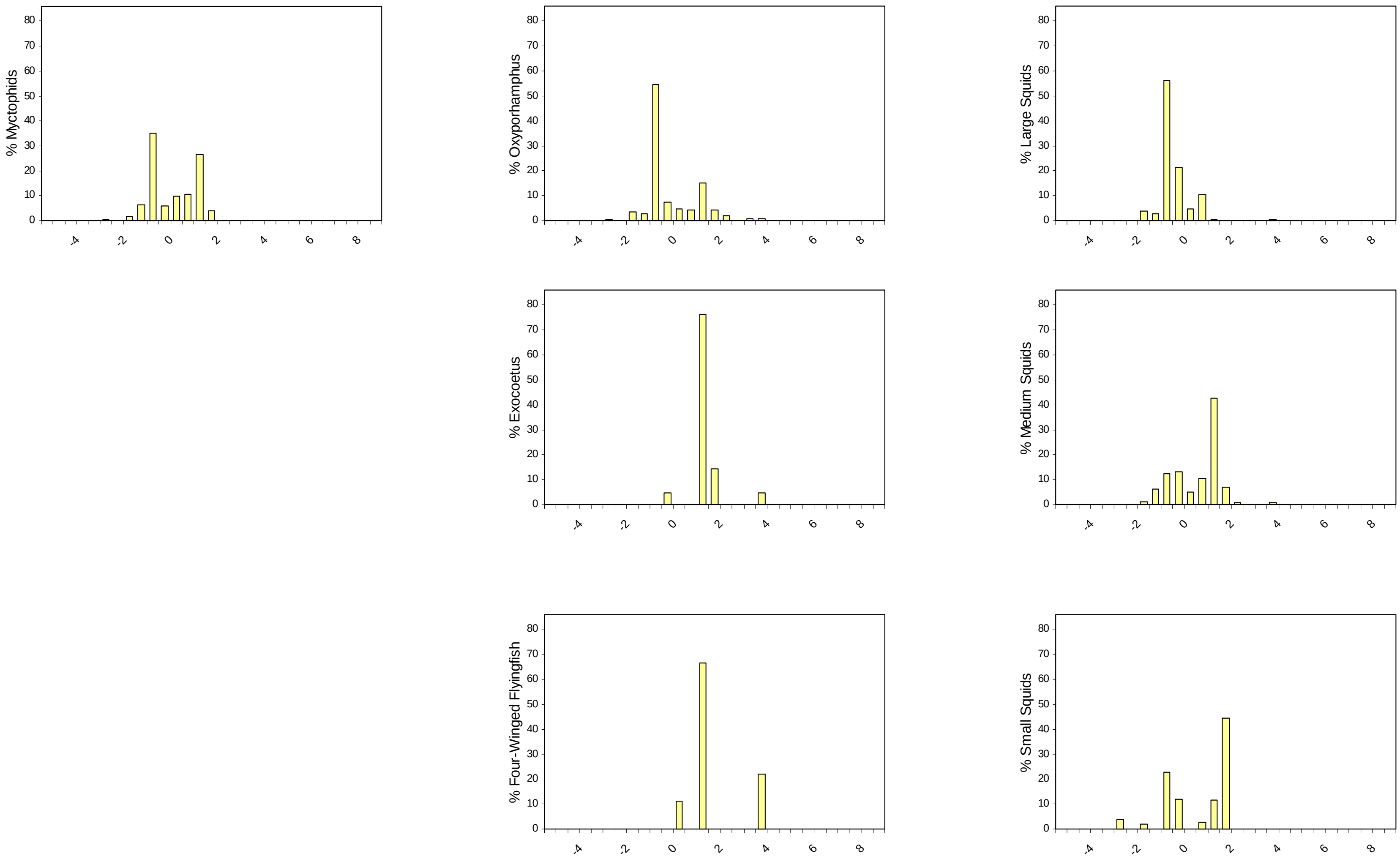
APPENDIX 1. Frequency histograms (by year), transformed to percentages, of the first two environmental axis scores where each of seven taxa of prey fishes and squids were sighted. Relationships are for the most part unimodal, thus validating an assumption of CCA.

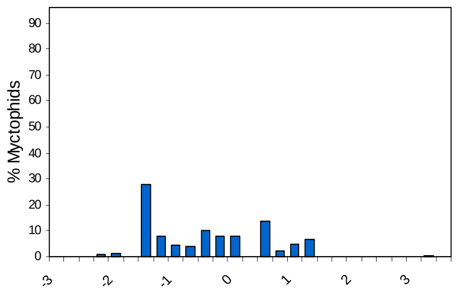
1986 Axis 1

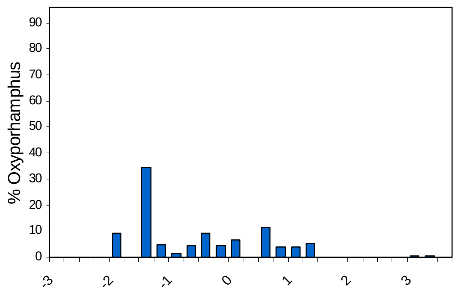


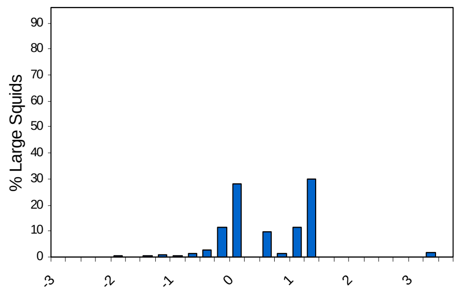
1986 Axis 2

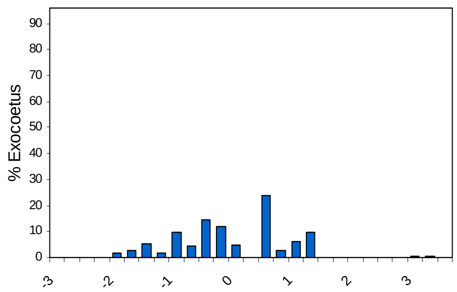

% Myctophids
% Oxyporhamphus
% Large Squids
% Exocoetus
% Medium Squids
% Four-Winged Flyingfish
% Small Squids
0
10
20
30
40
50
60
70
80
-4
-2
0
2
4
6
8

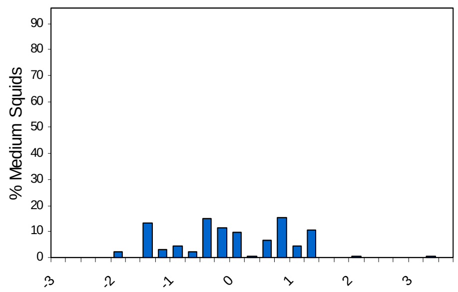
1987 Axis 1

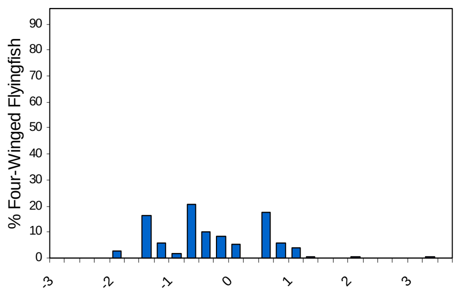

% Myctophids

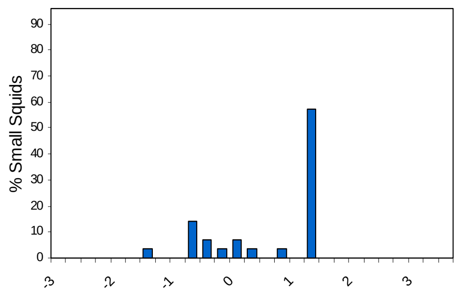

% Oxyporhamphus


% Large Squids

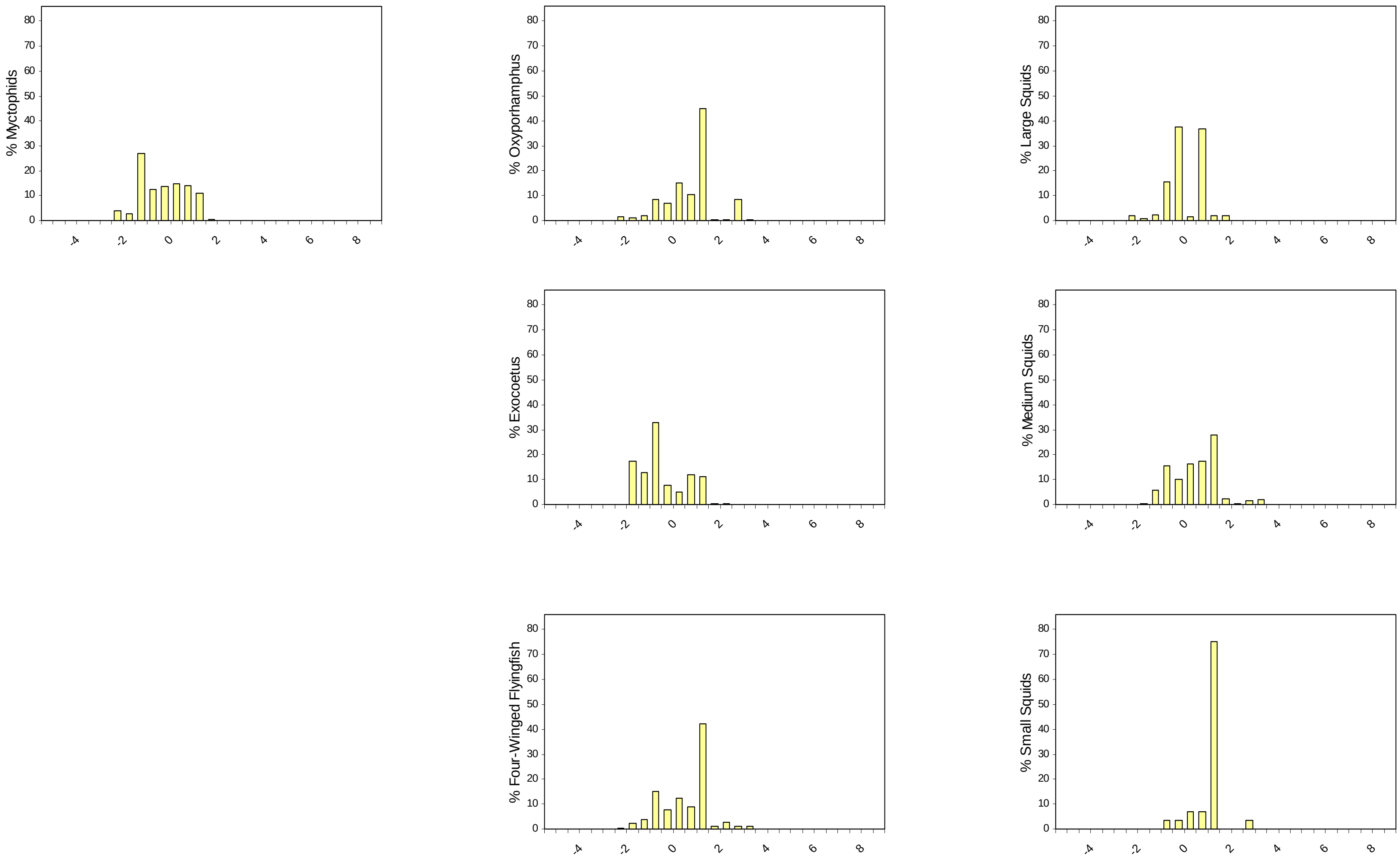

% Exocoetus


% Medium Squids

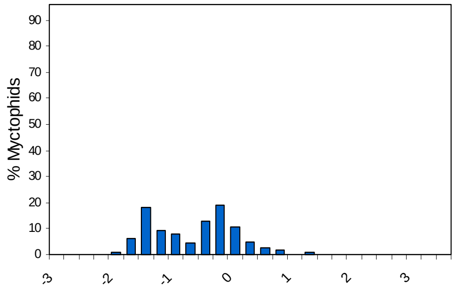

% Four-Winged Flyingfish

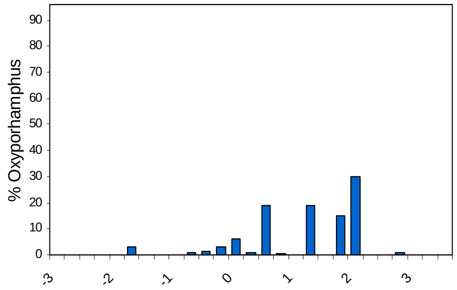

% Small Squids

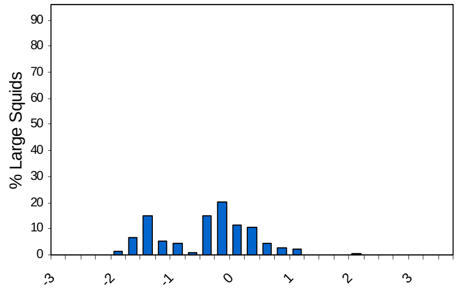
1987 Axis 2

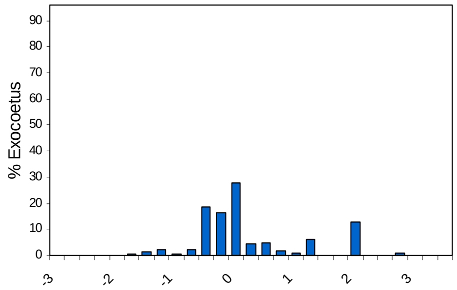

% Myctophids
% Oxyporhamphus
% Large Squids
% Exocoetus
% Medium Squids
% Four-Winged Flyingfish
% Small Squids
0
10
20
30
40
50
60
70
80
-4
-2
0
2
4
6
8

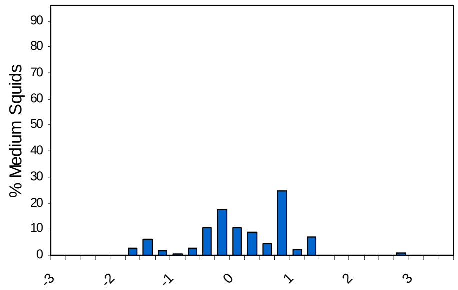
1988 Axis1

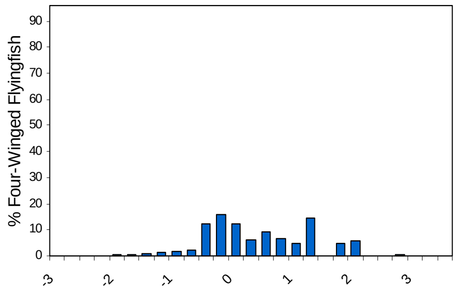

% Myctophids
90
80
70
60
50
40
30
20
10
0
-3
-2
-1
0
1
2
3

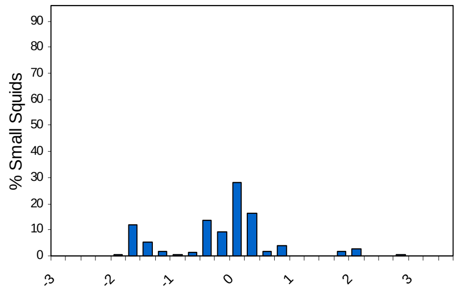

% Oxyporhamphus
90
80
70
60
50
40
30
20
10
0
-3
-2
-1
0
1
2
3


% Large Squids
90
80
70
60
50
40
30
20
10
0
-3
-2
-1
0
1
2
3

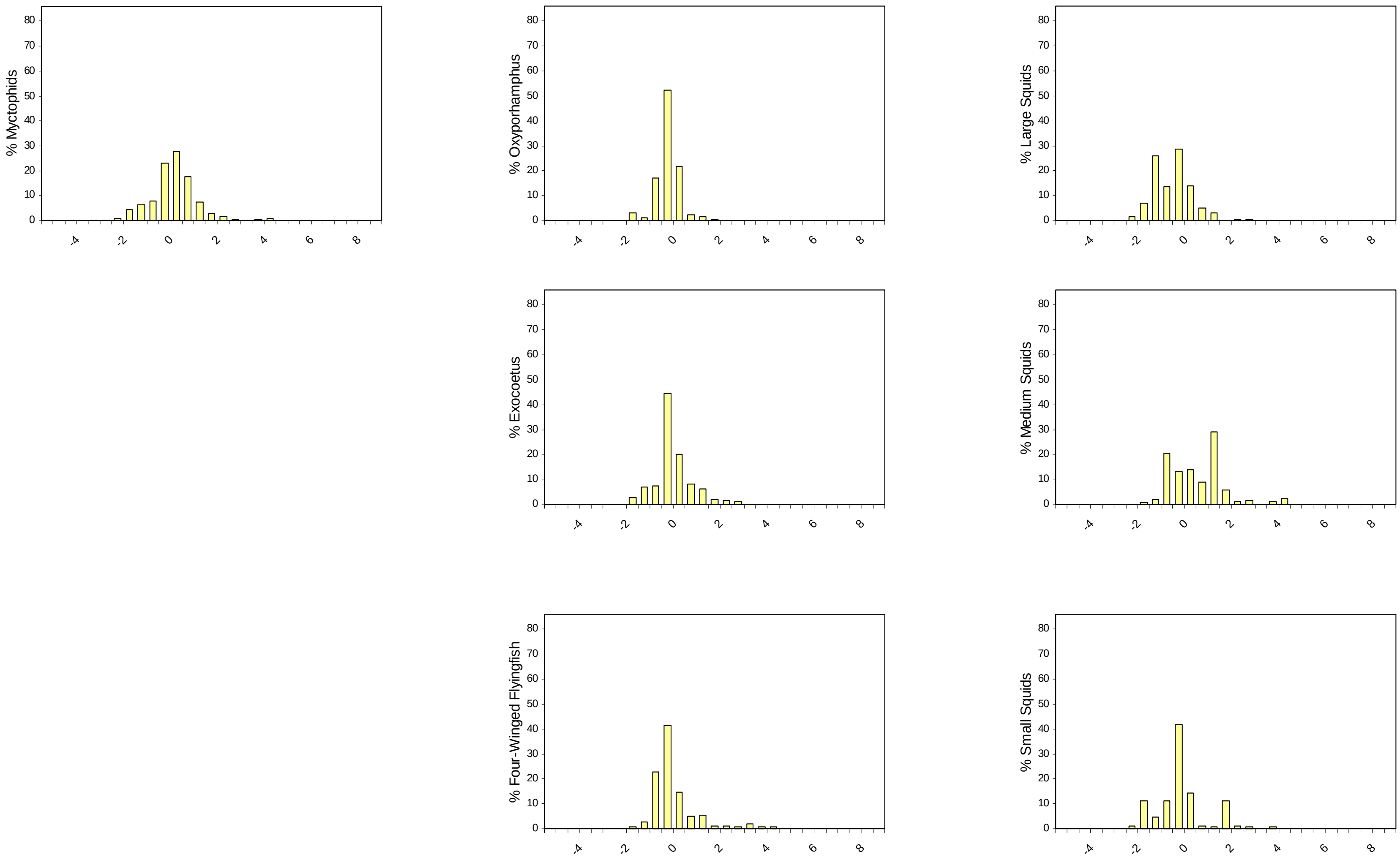

% Exocoetus
90
80
70
60
50
40
30
20
10
0
-3
-2
-1
0
1
2
3


% Medium Squids
90
80
70
60
50
40
30
20
10
0
-3
-2
-1
0
1
2
3


% Four-Winged Flyingfish
90
80
70
60
50
40
30
20
10
0
-3
-2
-1
0
1
2
3


% Small Squids
90
80
70
60
50
40
30
20
10
0
-3
-2
-1
0
1
2
3

1988 Axis 2


% Myctophids
% Oxyporhamphus
% Large Squids
% Exocoetus
% Medium Squids
% Four-Winged Flyingfish
% Small Squids
0
10
20
30
40
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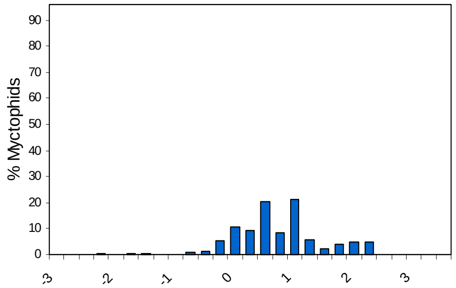
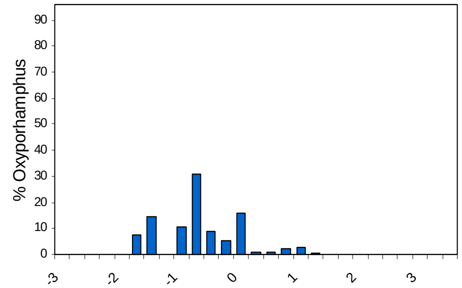
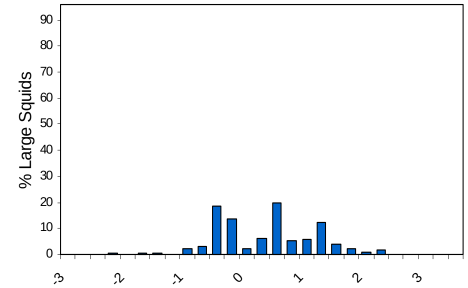
-4
-2
0
2
4
6
8

1989 Axis 1


% Myctophids
0 10 20 30 40 50 60 70 80 90
-3 -2 -1 0 1 2 3


% Oxyporhamphus
0 10 20 30 40 50 60 70 80 90
-3 -2 -1 0 1 2 3


% Large Squids
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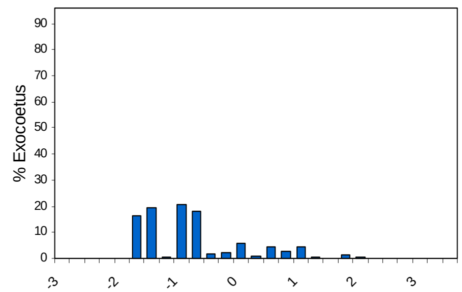
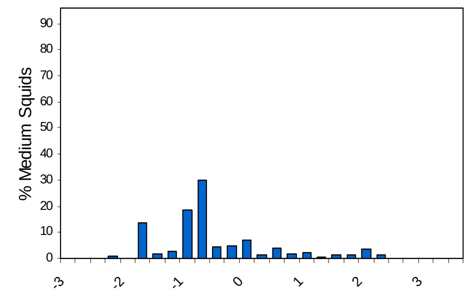
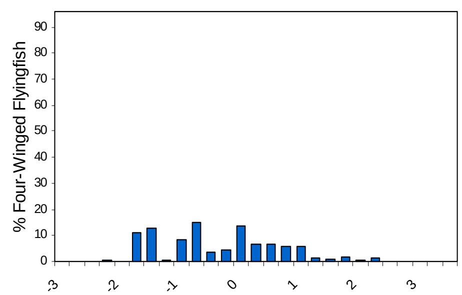
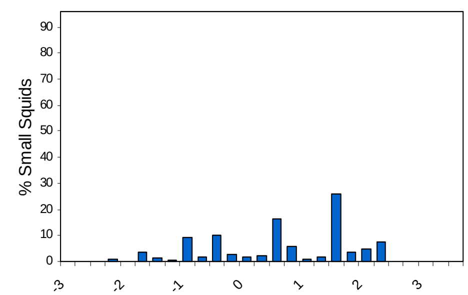
-3 -2 -1 0 1 2 3

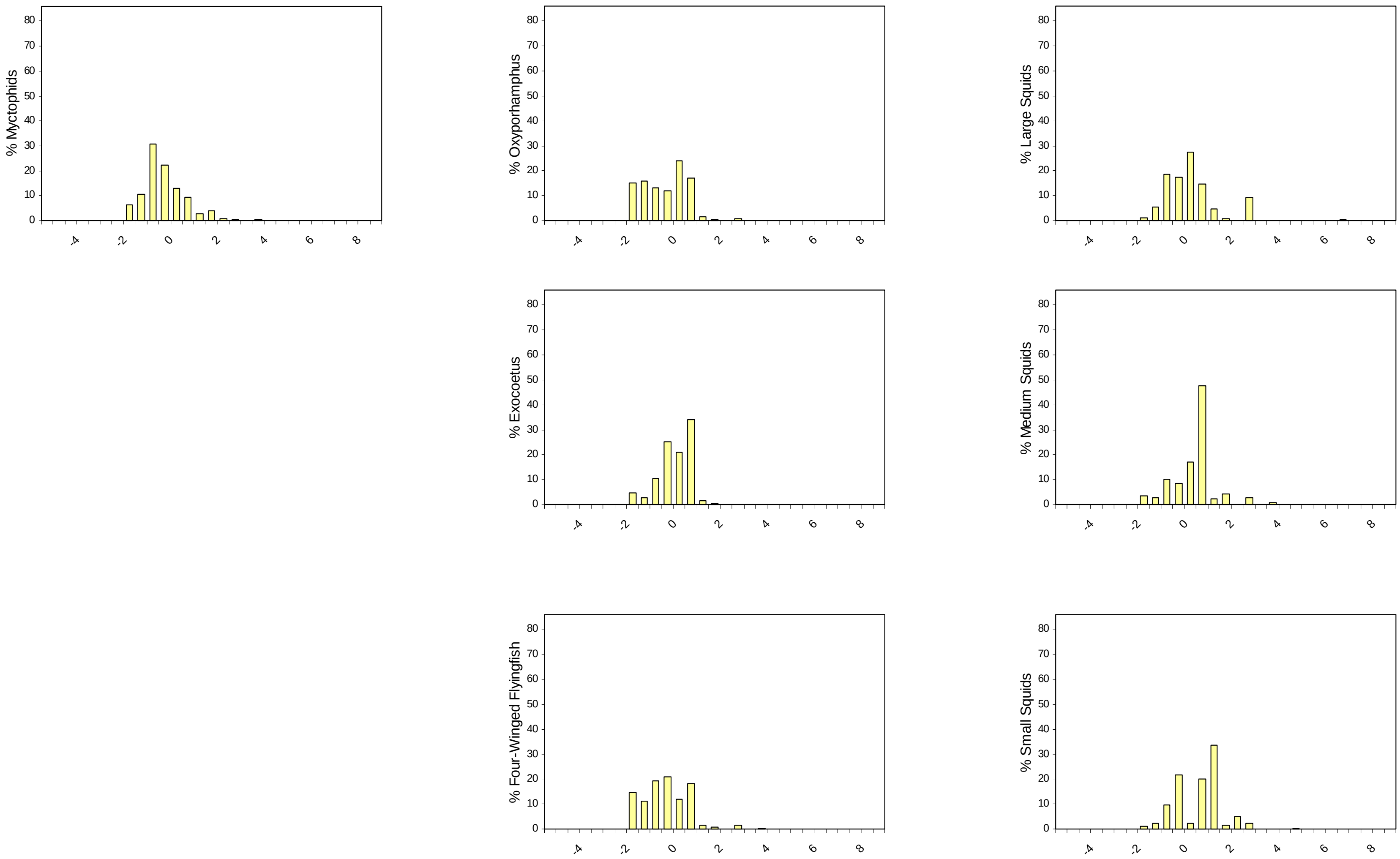

% Exocoetus
0 10 20 30 40 50 60 70 80 90
-3 -2 -1 0 1 2 3


% Medium Squids
0 10 20 30 40 50 60 70 80 90
-3 -2 -1 0 1 2 3


% Four-Winged Flyingfish
0 10 20 30 40 50 60 70 80 90
-3 -2 -1 0 1 2 3


% Small Squids
0 10 20 30 40 50 60 70 80 90
-3 -2 -1 0 1 2 3

1989 Axis 2



% Myctophids
% Oxyporhamphus
% Large Squids
% Exocoetus
% Medium Squids
% Four-Winged Flyingfish
% Small Squids
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-4
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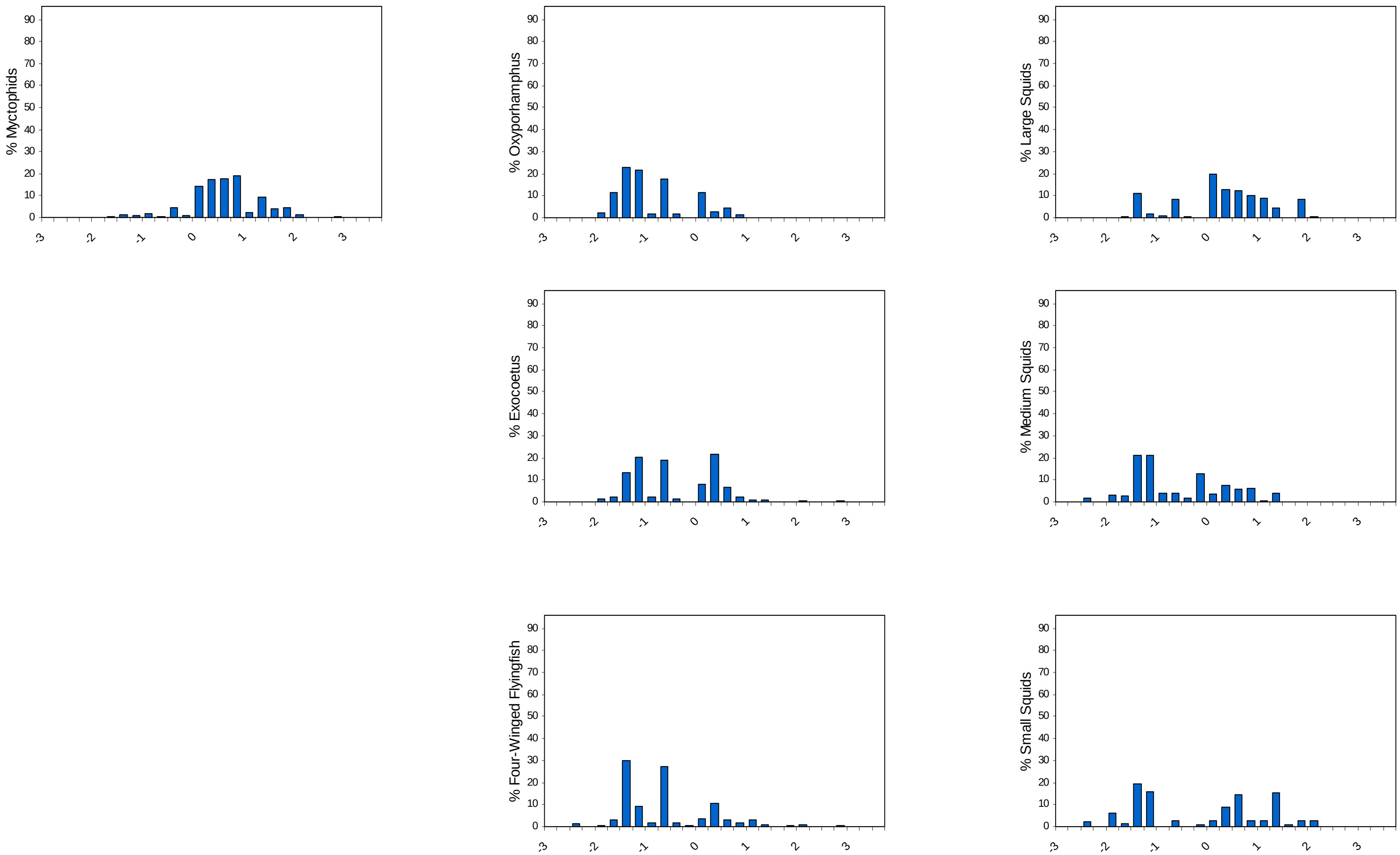
1990 Axis 1



% Myctophids
% Oxyporhamphus
% Large Squids
% Exocoetus
% Medium Squids
% Four-Winged Flyingfish
% Small Squids
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50
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70
80
90
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-2
-1
0
1
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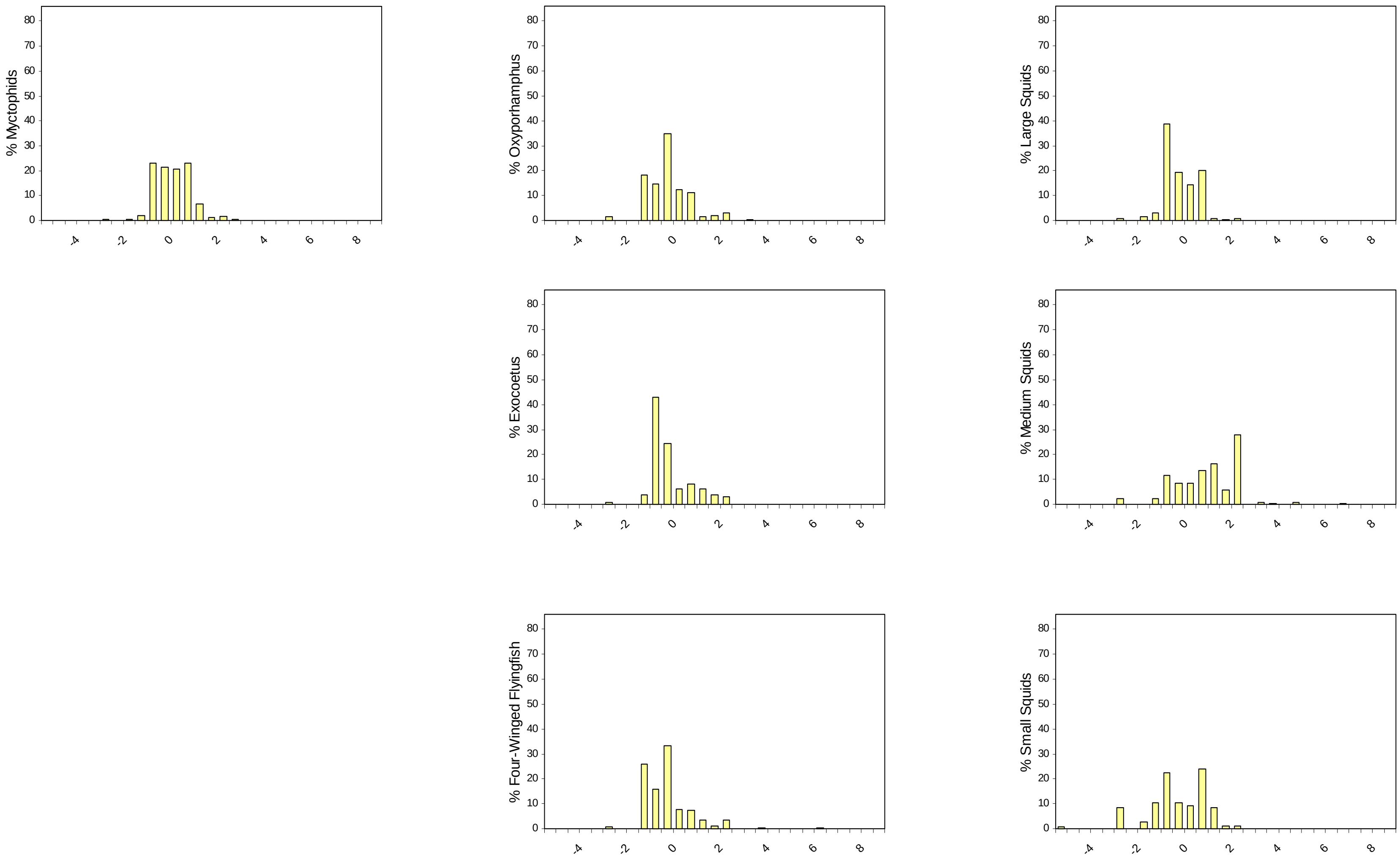
1990 Axis 2


% Myctophids
% Oxyporhamphus
% Large Squids
% Exocoetus
% Medium Squids
% Four-Winged Flyingfish
% Small Squids
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50
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70
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-4
-2
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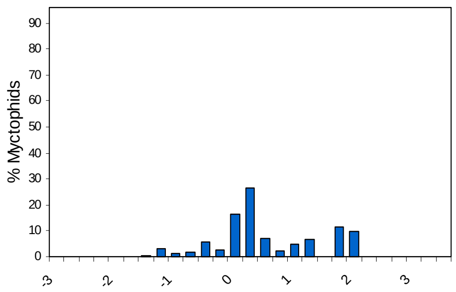
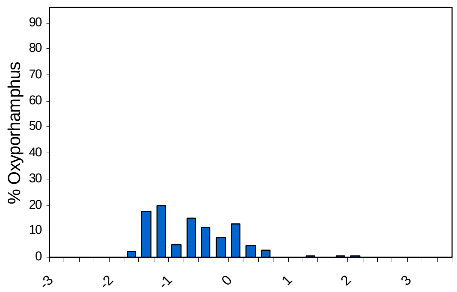
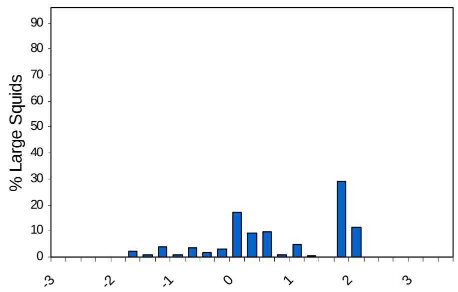
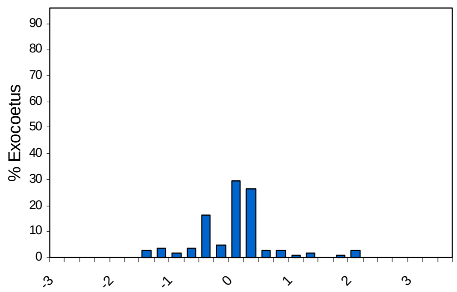
2
4
6
8

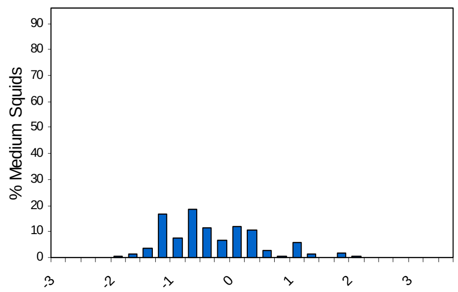
1998 Axis 1

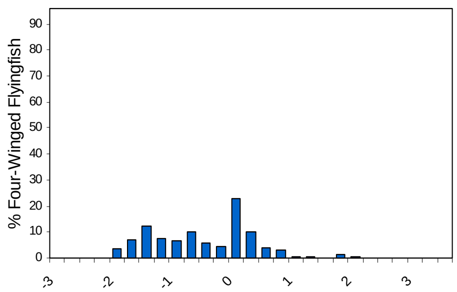

% Myctophids

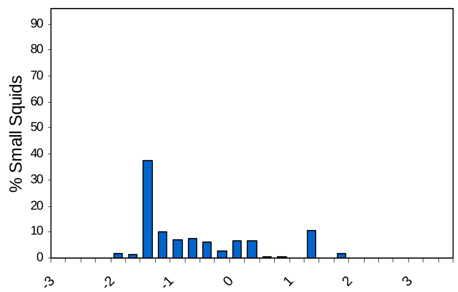

% Oxyporhamphus


% Large Squids

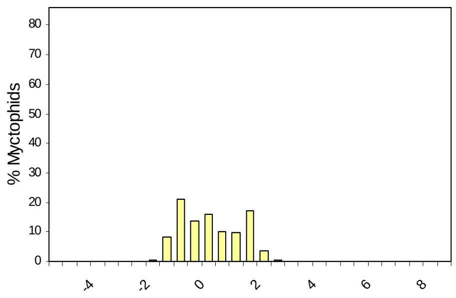

% Exocoetus

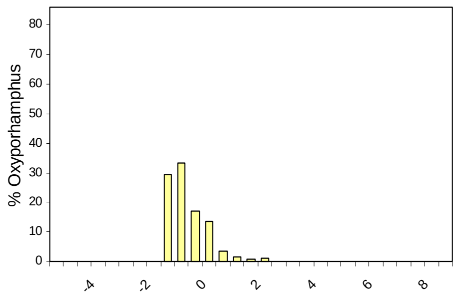

% Medium Squids


% Four-Winged Flyingfish


% Small Squids

1998 Axis 2


% Myctophids
0
10
20
30
40
50
60
70
80
-4
-2
0
2
4
6
8


% Oxyporhamphus
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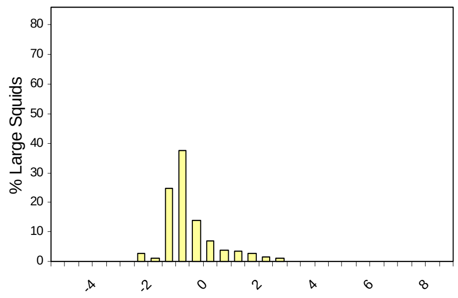
% Large Squids
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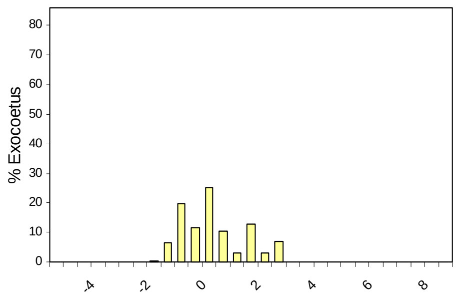
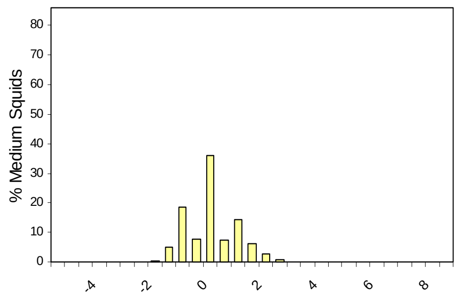
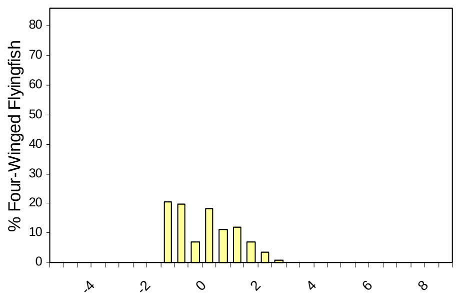
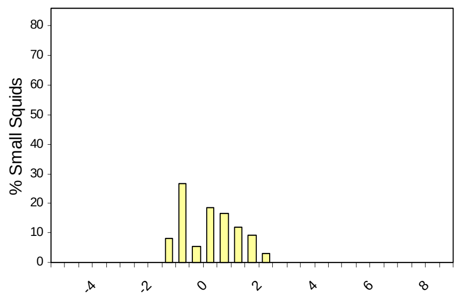
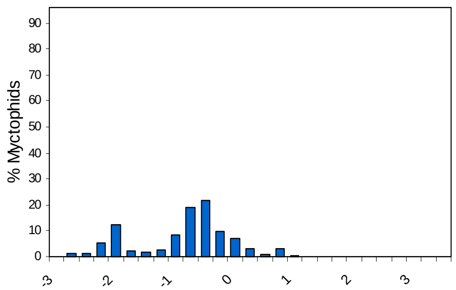

% Exocoetus
0
10
20
30
40
50
60
70
80
-4
-2
0
2
4
6
8

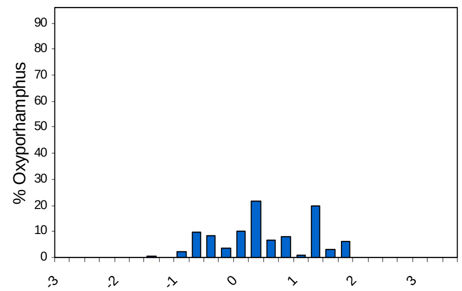

% Medium Squids
0
10
20
30
40
50
60
70
80
-4
-2
0
2
4
6
8

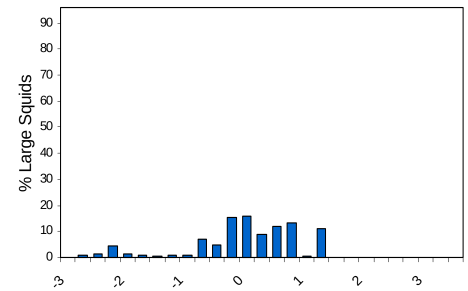

% Four-Winged Flyingfish
0
10
20
30
40
50
60
70
80
-4
-2
0
2
4
6
8

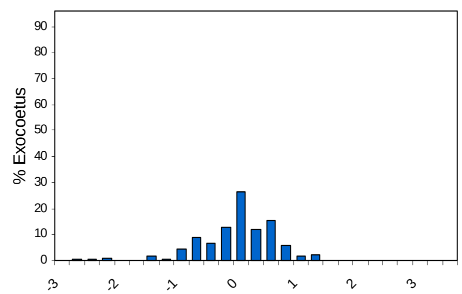

% Small Squids
0
10
20
30
40
50
60
70
80
-4
-2
0
2
4
6
8

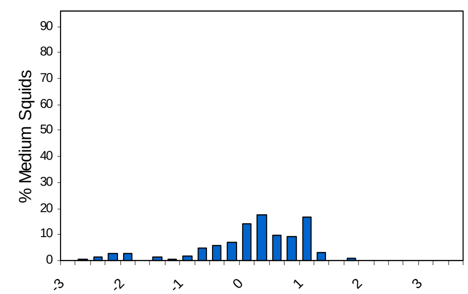
1999 Axis 1

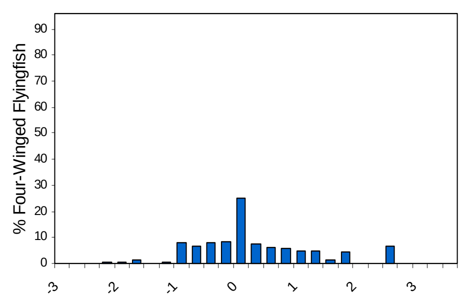

% Myctophids

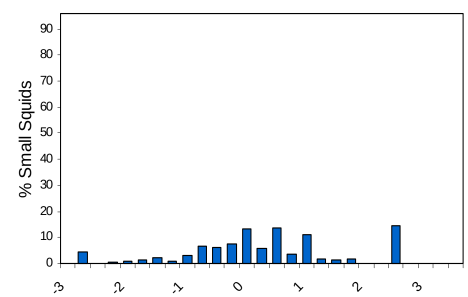

% Oxyporhamphus


% Large Squids

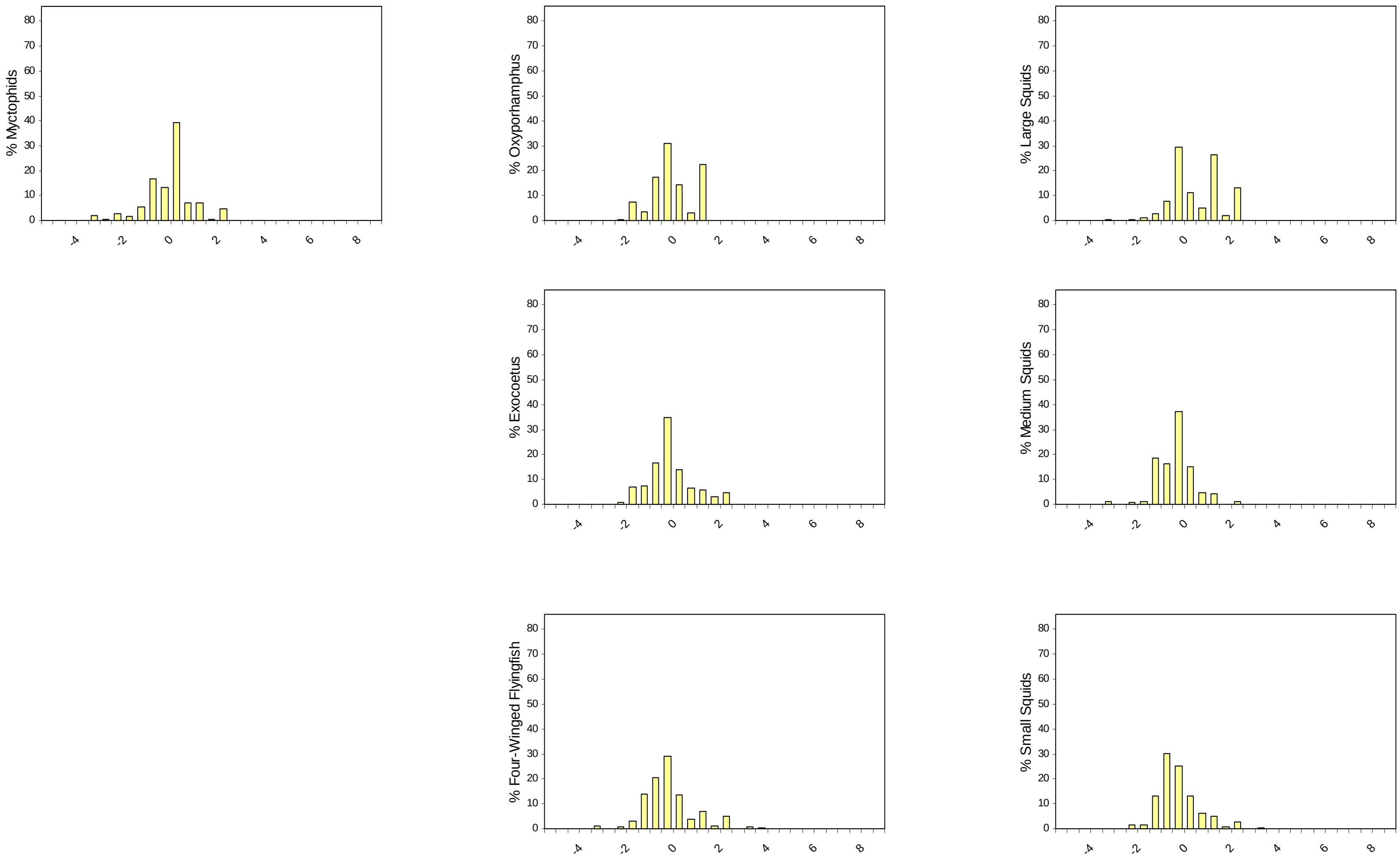

% Exocoetus


% Medium Squids

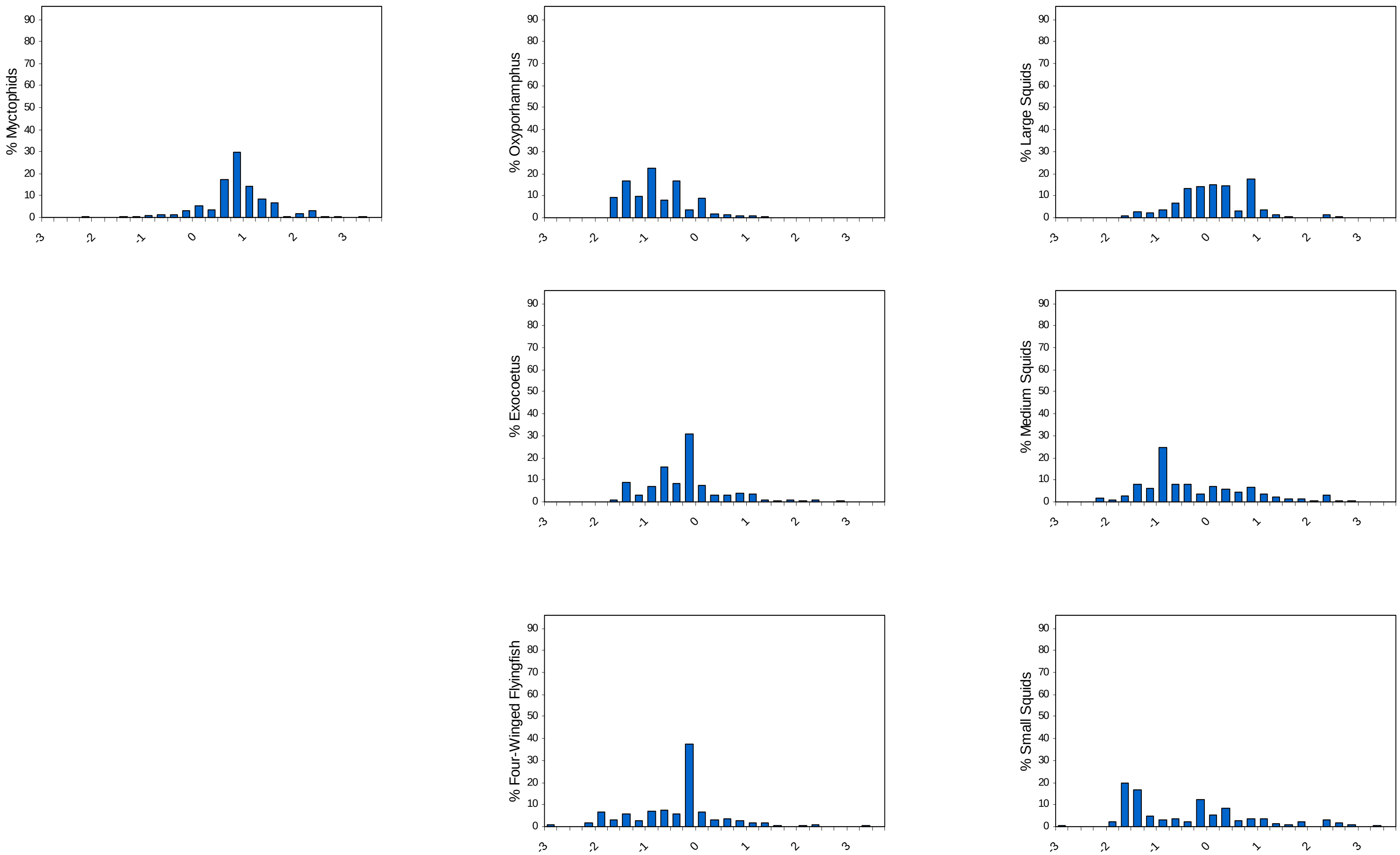

% Four-Winged Flyingfish


% Small Squids

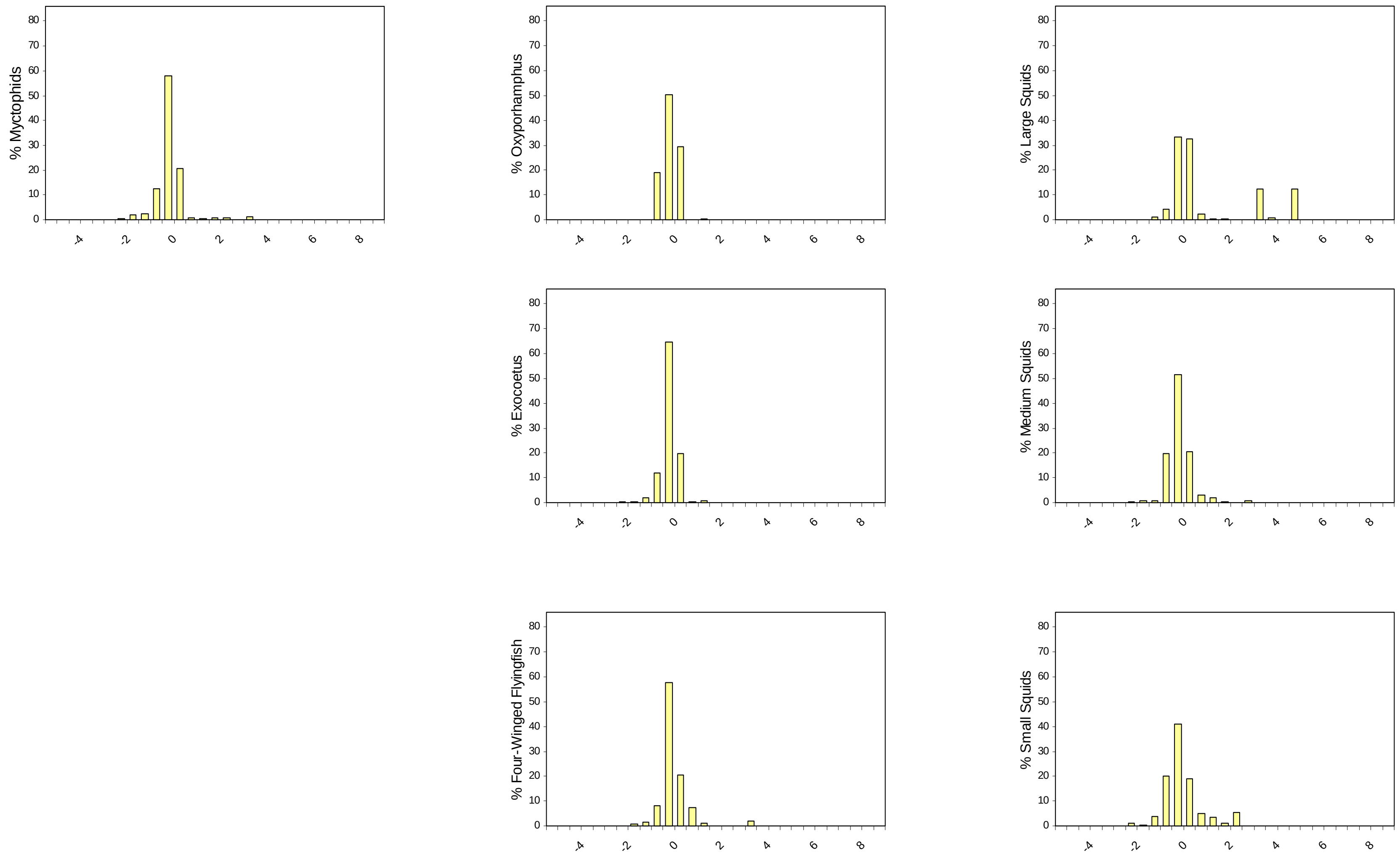
1999 Axis 2


% Myctophids
% Oxyporhamphus
% Large Squids
% Exocoetus
% Medium Squids
% Four-Winged Flyingfish
% Small Squids

2000 Axis 1


% Myctophids
% Oxyporhamphus
% Large Squids
% Exocoetus
% Medium Squids
% Four-Winged Flyingfish
% Small Squids
0
10
20
30
40
50
60
70
80
90
-3
-2
-1
0
1
2
3

2000 Axis 2


% Myctophids
% Oxyporhamphus
% Large Squids
% Exocoetus
% Medium Squids
% Four-Winged Flyingfish
% Small Squids
0
10
20
30
40
50
60
70
80
-4
-2
0
2
4
6
8

APPENDIX 2.

Responses to recommendations provided by the Center for Independent Experts review panel

Reviewer comments were extremely helpful and were incorporated into the current manuscript with the exception of those that fell into the categories below. The overall impression from all reviewers was that they were in agreement with the general conclusions of this paper, given the restricted time series of data available for analysis.

1. A number of reviewers made suggestions that would improve the presentation style of data or change the quantitative results, but which would not affect the qualitative conclusions of the analyses (see the following list). Due to time constraints, these suggestions were not incorporated into the present paper, but will be in future papers intended for publication in peer-reviewed journals.

   Oxenford: P. 12 bullets 2, 3, 4, 7 and 8; P. 13 bullet 1.
   Drinkwater: P. 5 bullets 1 and 2; P. 14 par. 2.
   Thompson: P. 11 item 5.

2. A number of valuable suggestions for additional analyses, using data not incorporated into the present paper, were made (see the following list). In particular, all reviewers placed strong emphasis on efforts to recover data collected by EASTROPAC cruises and to incorporate these into investigations of temporal patterns. Time constraints prohibit this at present, though efforts to recover these data are on-going and future investigations will include them.

   Oxenford: P. 12 bullet 5; P. 16 bullets 1 and 3; P. 17 bullet 1.
   Dower: P. 17 recommendation 2; P. 17 recommendation 3.
   Drinkwater: P. 3 bullet 1; P. 4 bullet 2; P. 7 bullet 2; P. 13 par. 3.
   Thompson: P. 8 par. 3.

3. A few reviewers suggested changes in analysis procedures for existing data, results of which may possibly change the qualitative conclusions of this research. As such, they deserve to be addressed specifically:

a) Oxenford (P. 16 bullet 4) suggests that data for all ecosystem studies be stratified into core and outer areas, and analyzed separately to look for temporal signals, particularly in the core area (key habitat of target dolphin species), that would not be confounded by spatial signals. Drinkwater (P. 6 bullet 2) and Thompson (P. 7 par. 3) make similar suggestions. We agree that this is a worthwhile approach, and in fact suggested such during the review. Time constraints do not allow such an approach to be incorporated into the current paper (the review comments were received with less than a month available to finalize ecosystem studies and have them published).

We will consider such stratification in future investigations. We do note however that oceanographic analyses indicate that temporal variation in the core area is much damped relative to the entire tropical Pacific (Fiedler 2002). If organisms have distribution and abundance patterns that reflect oceanographic conditions, as results of this paper indicate, the qualitative conclusions of analyses from the core area alone should be similar to conclusions reached in the current paper.

b) Dower (P. 17 recommendation 4) suggests that authors should explore whether the application of distribution-free statistical methods might offer a way to better deal with some of the sparse data series. Drinkwater (P. 20 bullet 1) makes a similar suggestion to use rank correlations. (These comments are presumably aimed at most or all of the ecosystem studies components.) We agree that this is a worthwhile exercise. Time constraints prohibit such investigations from being incorporated into the current paper, but we will consider this in future analyses.

c) Drinkwater (P. 7 bullet 1) suggests that additional analyses be performed with respect to temporal patterns in *variability* of various parameters (in addition to *mean* measures, which are currently incorporated). (This comment is presumably aimed at most or all of the ecosystem studies components.) This is a valuable suggestion and we intend to include such investigations in future analyses. Time constraints prohibit this approach from being incorporated into the present paper.

4. Finally, we do not agree with two comments and provide clarification below:

a) Drinkwater (P. 7 bullet 3) suggests that Generalized Additive Models be used to estimate abundance of prey fishes and squids. In fact, the raw data for these taxa do not constitute density values; they are merely categorical estimates of relative abundance. As such, we would have strong reservations with any attempt to convert these estimates into absolute abundance - which is the approach used for the seabird data.

b) Drinkwater (P. 14 par. 5) suggests that patchiness of prey fishes and squids be investigated. While this is certainly a valuable comment, the data used in our paper do not provide resolution to address this question of patchiness - as they are point estimates of relative abundance at a spatial scale of approximately one per 200 nautical miles. We do have additional data which might be used to investigate patchiness of a subset of the prey fishes and squids. These are continuous strip transect survey data of flyingfish flushed by the moving ship. A primary reason for instituting this survey was in fact to be able to quantify patchiness of these species. Future investigations will focus on this issue.